

2021-04-27

Landscape composition and configuration affect nest founding but not success of bumble bee colonies in agroecosystems in the Lower Mainland of British Columbia, Canada.

Kwafo, Richard

Kwafo, R. (2021). Landscape composition and configuration affect nest founding but not success of bumble bee colonies in agroecosystems in the Lower Mainland of British Columbia, Canada. (Master's thesis, University of Calgary, Calgary, Canada). Retrieved from <https://prism.ucalgary.ca>. <http://hdl.handle.net/1880/113341>

Downloaded from PRISM Repository, University of Calgary

UNIVERSITY OF CALGARY

Landscape composition and configuration affect nest founding but not success of bumble bee colonies in agroecosystems in the Lower Mainland of British Columbia, Canada.

by

Richard Kwafo

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE
DEGREE OF MASTER OF SCIENCE

GRADUATE PROGRAM IN BIOLOGICAL SCIENCES

CALGARY, ALBERTA

APRIL, 2021

© Richard Kwafo 2021

ABSTRACT

Landscape structure influenced by land-use is likely to affect pollinator demography. Using naturally colonized nest boxes placed at 27 sites in the Lower Mainland of British Columbia, I assessed demographic responses of bumble bees to the availability of resources as inferred from landscape structure (i.e., landscape composition and configuration), and examined the spatial scale that best explained responses to the landscape. I used mixed model regression analysis to model the influence of semi-natural habitat, beneficial agriculture, suburban cover, and habitat edge density, all measured in six radii (250 m - 2500 m) around colonies, on nest founding and success of bumble bee colonies. Semi-natural habitat had no relationship with nest founding and colony success. Nest founding decreased in surroundings with more “beneficial agriculture” cover (i.e., mass flowering berry crops), however, nest founding increased at locations with more edge habitats. Higher amount of suburban cover decreased nest founding. Nest founding was best explained by the landscape at a 1500 m radius around the nest, however, there was no evidence of colony success responding to the landscape at any spatial scale. I conclude that beneficial agriculture and suburban cover had negative consequences for nest founding in bumble bee populations within my study landscape. Edge habitats seemed to attract more bumble bee queens to nest and may maintain bee populations while serving as sources of wild bumble bee pollinators, who might forage within nearby commercial blueberry crops to improve crop yield.

ACKNOWLEDGEMENTS

I would like to thank my supervisors Paul Galpern and Ralph Cartar for their guidance and support. I am grateful for the opportunity to return to my entomological roots and explore the world of “6 legged” creatures. I would like to thank my committee members Jana Vamosi and John Post for their helpful feedback and thoughtful advice.

I thank Rebecca Tyson and NSERC for providing funding, which made this project possible and especially to Rebecca Tyson for her warm reception, advice, and contributions in making this project a reality. Many thanks to Aime Messiga for his advice, support, and encouragement and for making it possible for me to carry out part of my research at the AAFC (Agassiz) field station. I am grateful to Carine Bineng for her support with field logistics.

I want to thank my field assistant Michael Gavin for his hard work during the field season. I also want to thank Sam Robinson for his valuable lessons in R.

I would like to thank Blueberry growers in the Lower Mainland of BC for allowing me to use their farms for this project. I thank Eric Gerbrandt and Mark Sweeney for facilitating valuable connections with blueberry growers.

Lastly, I would like to thank my family and loved ones for putting up with my absence and for supporting me throughout this endeavour. May God bless you all.

TABLE OF CONTENTS

Contents

ABSTRACT.....	ii
ACKNOWLEDGEMENTS	iii
TABLE OF CONTENTS.....	iv
LIST OF TABLES	v
LIST OF FIGURES	vii
CHAPTER 1	1
GENERAL INTRODUCTION.....	1
CHAPTER 2	5
INTRODUCTION	5
METHODOLOGY	13
Field sites	13
Bumble bees.....	13
Landscape	14
Data analysis	17
RESULTS	19
Nest founding.....	19
Colony success.....	19
Spatial scale of response.	20
DISCUSSION	20
Effect of the landscape on nest founding and colony success.	20
Spatial scale of response.	26
CONCLUSIONS.....	28
CHAPTER 3	30
GENERAL CONCLUSIONS	30
LITERATURE CITED	49

LIST OF TABLES

Table 1: Detailed land cover used in the regression analysis. Land use types were clustered into groups to form a single habitat category. Quantification was based on AAFC crop inventory data. Habitat categories were quantified within a 2500 m radius of bumble bee colony. The proportion of cover type, edge density per cover type, mean \pm SD (cover area), minimum and maximum cover area are given for 27 study locations.	42
Table 2: Mean and standard deviation (proportional) of edge for each pair of land cover classes where edge represents the interface between habitat types. The mean and standard deviation are given for a combination of land cover classes for 27 study locations and quantified within a 2500 m radius of bumble bee colony.	43
Table 3: Principal Component Analysis (PCA) showing eigenvector scores, Box-Cox exponents applied to transformations and constants added to measures of colony success before power transformation, and the proportion of variance in original data explained by the principal component axis. PCA was used to produce a single measure of colony success that summarized six measures of colony success.	45
Table 4: Nest founding model. Mixed model logistic regression predicting nest founding from the proportion of beneficial agriculture, edge density, the proportion of semi-natural habitat and the proportion of suburban cover. The table shows average parameter estimates and standard error (SE), z value and p-value for all parameters estimated in the models fitted at each spatial scale (250 m to 2500 m, 106 boxes and 27 sites). All continuous predictors are standardized. Marginal R^2 values are presented as measures of model fit and consider fixed effects only. Site identity was a random effect. Significant parameters are bolded. AIC _C and delta AIC _C scores for the full model at each scale in comparison with its null model.	46
Table 5: Colony success model. Generalised linear mixed model (gaussian distribution) predicting nest success from the proportion of beneficial agriculture, edge density, the proportion of semi-natural habitat, the proportion of suburban cover and the interaction between beneficial agriculture and edge density. The table shows average parameter estimates and standard error (SE), denominator degrees of freedom, t value and p-value for all parameters estimated in the models fitted at each spatial scale (250 m to 2500 m, 63 boxes, 23 sites). All continuous predictors are standardized. Marginal R^2 values are presented as measures of model fit and consider fixed effects only. Site identity was a random effect. Significant parameters are bolded. AIC _C and delta AIC _C scores for the full model at each scale in comparison with its null model.	47

Table 6: Model comparison using AIC_C and model weight for the models on nest founding in relation to landscape fitted at each spatial scale (250 m to 2500 m). Models are presented in order with the first model being the best among the list of the models compared according to its lowest delta AIC_C and highest AIC_C weight value. Delta AIC_C represents the differences in the AIC_C score relative to the minimum AIC_C , K represents the number of parameters in the model, AIC_C weight is the proportion of the total amount of predictive power of the set of models being compared, cumulative weight is the sum of delta AIC_C weight, log-likelihood describes how plausible the model is, given the data. 48

Table 7: Model comparison using AIC_C and model weight for the models on colony success in relation to landscape fitted at each spatial scale (250 m to 2500 m). Models are presented in order with the first model being the best among the list of the models compared according to its lowest delta AIC_C and highest AIC_C weight value. Delta AIC_C represents the differences in the AIC_C score relative to the minimum AIC_C , K represents the number of parameters in the model, AIC_C weight is the proportion of the total amount of predictive power of the set of models being compared, cumulative weight is the sum of delta AIC_C weight, log-likelihood describes how plausible the model is, given the data. 48

LIST OF FIGURES

Figure 1: Bumble bee colony cycle and the availability of floral resources provided by blueberry crops. Blueberry crops provide copious floral resources after nest founding and early in the period of colony development (i.e., production of first brood), however, crop bloom ceases during the period of colony growth (i.e., production of more workers, increase in colony size) and up to the production of reproductives (i.e., new queens and males). Images from google images.	33
Figure 2: Location of study sites (n= 27) in the Lower Mainland, British Columbia, Canada. Land cover types were quantified using AAFC crop inventory satellite imagery (Annual Space-Based Crop Inventory for Canada 2019). From its original ~ 45 cover type classification, the raster imagery was reclassified by clustering classes into three groups: semi-natural cover (forest, shrubland, pasture, grassland, and wetlands), beneficial agricultural cover (blueberry, raspberry, and cranberry fields) and suburban cover (residential and built-up areas). The category on non-beneficial agriculture (maize, cereal, wheat, etc.) was excluded from the analysis, however, it is included in this figure for clarity on the range of land cover classes in the satellite imagery.	34
Figure 3: Visual (a) representation of edge habitats as shared margins (light green) between two land cover classes (b) edge habitat represented as grassy margins (location within red outline) (c) edge habitat represented as hedgerows with herbaceous vegetation (d) edge habitat represented as grassy margins with remnant herbaceous vegetation. Images from google earth imagery.	35
Figure 4: Edge amount (proportional sum) for each pair of land cover classes where edge represents the interface between habitat types. The sums are given for a combination of land cover classes for 27 study locations and quantified within a 2500 m radius of a bumble bee colony. Blue bars represent edges that are controlled by farmers.	36
Figure 5: Four representative study sites with land cover types nested in six spatial scales (250 m, 500 m, 750 m, 1500, 2000 m, 2500 m) used in the analysis.	37
Figure 6: (a) An example of a location along ditch banks or uncultivated areas close to blueberry farms where underground boxes were placed, (b) Bumble bee nest lined with upholsterers' cotton to provide insulation and medium for nest establishment (c) Bumble bee box placed a few centimetres below the surface of the ground. (d) Bee box covered with excavated sod with a PVC tube leading to the nest and serving as entrance and exit route for bumble bee queen and workers.	38
Figure 7: Partial regression plot of nest founding (black line) and the 95% confidence interval (grey region) describing the nest founding model at a 750 m spatial scale. This result supports the prediction	

that the proportion of beneficial agriculture in the landscape is negatively related to nest founding. Circles show data (N= 106)..... 39

Figure 8: Partial regression plot of nest founding (black line) and 95 % confidence interval (grey region) describing the nest founding model at a 2500 m spatial scale. This result is against the prediction that the proportion of suburban cover in the landscape is positively related to nest founding. Circles show data (N= 106)..... 40

Figure 9: Partial regression plot of nest founding (black line) and the 95% confidence interval (grey region) describing the nest founding model at a 1500 m spatial scale. This result supports the prediction that edge density in the landscape is positively related to nest founding. Circles show data (N= 106)..... 41

CHAPTER 1

GENERAL INTRODUCTION

From the perspective of landscape ecology, the terrestrial landscape can be understood as a mix of land covers in which animals complete their life cycles (Doligez et al. 2008). The landscape structure is determined by (a) landscape composition (the types of land cover, their proportional areas) and (b) landscape configuration (the proximity of cover types to one another). Landscape composition and configuration are factors likely to influence the abundance and diversity of animals, by determining the quantity, quality and accessibility of resources in the landscape (Dunning et al. 1992, Taylor et al. 1993). Thus, understanding the effects of the landscape structure on animals can suggest conservation actions such as retaining or enhancing land covers that provide important habitats, or changing landscape configuration to ensure that different land covers needed by focal organisms are accessible to them (Fahrig et al. 2015).

In temperate areas, agricultural landscapes are characterised by a mosaic of semi-natural cover, crop fields of small to large field sizes, increased crop-to-crop field adjacencies, low crop diversity, and monoculture production for ease of management and reduced cost of production (Matson et al. 1997). Intensive agriculture, driven in part by growing demand from a hungry world, is a leading cause of the loss of natural habitat and one of the causes of species loss (Tilman 1999, Tscharntke et al. 2012). Agricultural expansion negatively affects animal populations through the loss of foraging resources, as well as other key habitats such as nesting sites (Potts et al. 2010). For bees, the subject of this thesis, agricultural landscapes often have insufficient forage availability and a lack of continuity in floral resources throughout the flight season, both of which can negatively affect populations (Tscharntke et al. 2005, Landis 2017, Proesmans et al. 2019).

Over a third of crops rely directly on animal pollination (Klein et al. 2007). Across the globe, pollination services in agriculture are provided by managed honey bee *Apis mellifera* (McGregor 1976, Watanabe 1994) and by wild bees including *Bombus* sp. (Klein et al. 2007). The pollination service input supplied by bees to agricultural production forms an important economic sector and contributed to an

estimated US\$ 200 billion global pollination services annually (Gallai et al. 2009, Vaidya et al. 2018). Pollinators, while moving pollen across and among individual plants, also increase the quantity of pollen deposited on stigmas and increase the seed set, quantity and quality of crops, as well as their market value (Isaacs and Kirk 2010).

Wild pollinators have received considerable attention for their role in crop pollination and their ability to reduce pollination deficits (Button and Elle 2014). Particularly, pollinators such as bumble bees are considered efficient pollinators than honey bees, because of their ability to sonicate. Highbush blueberry plants (*Vaccinium corymbosum*) for example, require that their anthers be sonicated before the release of pollen during floral visitation by pollinators (Cardinal et al. 2018). Even though honey bees are widely used for blueberry pollination, sonication behaviour needed to ensure the effective release of pollen is performed by bumble bees, which makes them efficient pollinators of blueberry crops (Javorek et al. 2002). Wild bees provide essential crop pollination, however, this important ecosystem service is at risk due to the decline in wild bees as a result of agricultural intensification (Kremen et al. 2002). Wild bumble bee abundance, diversity and colony success are directly related to the availability of forage and nest sites, which are largely dependent on the structure of the surrounding landscape (Hines and Hendrix 2005, Holzschuh et al. 2010, Gervais et al. 2020). It is therefore important to understand the effect of the structure of the landscape on pollinators, especially within agricultural landscapes.

Land-use pattern can affect the spatial structure of the landscape. The effect of landscape composition and configuration on pollinators, as reported in the ecological literature, focuses on the roles of crop cover and non-crop cover, including semi-natural cover. Semi-natural land covers in agricultural landscapes are considered to be important sources of forage such as nectar and pollen and nesting sites, which can positively influence the growth of pollinator colonies and their reproductive success (Crone and Williams 2016, Spiesman et al. 2017, Proesmans et al. 2019). Semi-natural land covers also supply important over-wintering sites for pollinators. Crop fields especially those that host mass-flowering crops can provide a novel source of forage for pollinators (Yang et al. 2008, Diekötter et al. 2014). Because of

their enormous floral bloom, mass-flowering crops like oilseed rape (canola) and blueberry can constitute a huge payoff for foraging wild bees, likely increasing bee populations (Holzschuh et al. 2013).

On the other hand, contrasting results have been reported on the effects of landscape configuration. Martin et al. (2019) found positive effects on pollinator abundances, while others have found no support that landscape configuration measured as edge density influenced pollinator communities (Holzschuh et al. 2010). Margins in agricultural landscapes, as an interface between habitat types, are often accompanied by strips with herbaceous, woody or grassy vegetation that resemble semi-natural habitat and provide forage and nesting sites for pollinators (Stanley and Stout 2013). Because these linear features support a wide range of diverse plant communities that are not abundant in adjacent habitats (Del Barrio et al. 2006), landscapes that have a high density of edge habitats can support diverse pollinator groups due to the availability of complementary forage and nest sites (Osborne et al. 2008b).

Several traits of wild bees make them excellent candidates to explore the importance of the landscape structure on populations in an agricultural landscape. Bees are central place foragers that nest and forage in the same or different habitats allowing for the exploration of the effect of the landscape on nesting and reproduction (Goulson et al. 2002, Williams and Kremen 2007). However, the persistence and survival of wild bees, like most other animals, may rely on their ability to access high-quality resources in the landscape where they live. Bees require distinct resources such as nesting substrate, nesting material and foraging resources (Heinrich 1979). These resources vary in their distribution among different habitats in space and time (Westrich 1996). Therefore, factors such as the identity and amount of different habitat types, the resources they provide, and the spatial distribution of these habitats, can influence measures of bee demography (Williams and Kremen 2007, Williams et al. 2012). When the structure of a given landscape has been modified by humans to become a mosaic of natural and human-dominated land covers, the abundance and distribution of resources and their variation in space and time may be affected. In agricultural landscapes, for example, those with mass-flowering crops, remnant semi-natural habitats provide floral resources that last the season, while, mass-flowering crops provide a pulse of floral resources for a short period in the season (Westphal et al. 2003, Proesmans et al. 2019). Wild bees living in such

landscapes can forage on flowers from semi-natural habitats, but at the same time, can potentially benefit from resource blooms from mass-flowering crops.

In this thesis, I examine the effect of the landscape structure on nest founding and colony success of individual bumble bee colonies in an agricultural landscape. In particular, this thesis asks: (1) are nest boxes occupied in a manner that can be explained by metrics of landscape structure, such as compositional measures of the proportional area of land cover, or by configurational measures such as edge density? (2) does the success of individual bumble bee colonies relate to the landscape structure? (3) at what spatial scale surrounding a colony does the landscape structure matter most for nest founding and colony success? By understanding how the landscape affects wild bumble bees and the factors that predict colony founding and success, this study intends to inform management practices for maximizing the availability of bees in the vicinity of a pollen-limited crop. For instance, if I were to find that the proportion of semi-natural land cover, were to be positively associated with nest founding and colony success, land-use decision-makers, such as farmers, may choose to retain, restore, or augment this land cover, and do so at a scale that maximizes the potential success of their crops. Such management strategies within or near fields could enhance visitation by wild bumble bee pollinators to the crop when it is in bloom, potentially leading to improved crop yields.

CHAPTER 2

INTRODUCTION

The availability and distribution of resources (i.e., food, nest sites) in the landscape can determine species population densities and community assemblages (Dempster and Pollard 1981, Finstad et al. 2009). When food and nest sites are abundant in the landscape, the fitness of individuals can be positively affected. However, reductions in the quantity and quality of food, or disturbances that limit access to high-quality habitat, can negatively impact population demographics (Lin and Batzli 2001).

For organisms, resource availability is likely to be determined by the composition and configuration of their landscape, where composition refers to the relative proportion and the type and diversity of land covers, and configuration refers to the spatial arrangement of a given land cover type in the landscape (Fahrig and Merriam 1994). Composition and configuration thus define the structure of the landscape, and these are commonly assessed by analyzing satellite-based imagery to identify classes of land cover, where the class is used as a proxy for a type of habitat, considered important for a focal species or group of species. Landscape composition and configuration have also been associated with species interactions (Fahrig et al. 2011). For instance, the relative amount of a type of habitat (or class of land cover), the proximity of a patch of a certain habitat relative to another, and the adjacencies of habitat patches of different classes may determine the quantity, quality and accessibility of resources in the landscape (Fahrig et al. 2011). Land-use pattern affects the structure of the landscape, for example, a decrease in the amount of one or more habitat types can limit the availability of resources. Equally, isolation as a result of decreased connectivity between habitat patches can affect an organisms ability to access resources in the landscape, leading to negative consequences for population demographics (Jonsen and Fahrig 1997). Thus, we might expect that the structure of the landscape has the potential to affect organisms and populations that live there. A corollary, potentially advantageous for conservation purposes is that by changing the landscape structure it may be possible to boost the viability of a population. For this reason, it is useful to evaluate the effects of

landscape structure to understand the mechanisms that drive the relationship between the landscape and an organism.

An additional consideration when examining the effect of the landscape structure on a population is the spatial scale at which the landscape is experienced by the population. Habitat variation exists at different spatial scales. Studies suggest that an animal (i.e., an individual) interacts with the environment at small scales but may also be influenced by the presence and pattern of resources at large spatial scales (i.e., a “landscape” scale) (Wiens 1989). For animals, the spatial extent and importance of these scales may depend on the size, behaviour and life history of the animal (Holland et al. 2005, Gaillard et al. 2010). Thus, an animal’s response (e.g., abundance) may vary at different spatial scales as patterns observed may be influenced by processes operating at different scales or interacting across multiple scales (Holland et al. 2004, Martin and Fahrig 2012). If the relationship between the landscape structure relative to an animal’s response is scale-dependent, then analysis at multiple spatial scales is a necessary approach to detect which one matters biologically (Wiens and Milne 1989). Adopting a multi-scale approach to studying an animal’s relationship to its environment may be a means of identifying the scales of environmental variation (e.g., the spatial extent or the grain at which land cover pattern is measured) that influence the observed responses.

Intensive agriculture is an important source of landscape structure, influencing the pattern of land covers (Kerr and Deguise 2004). As a consequence of the demand for food to feed growing global populations, agricultural land-uses are expanding rapidly (Fróna et al. 2019). An agricultural landscape can be viewed as a mosaic of habitat patches distributed across the landscape (e.g., agricultural land-use patches like cropland and pasture, and natural or semi-natural patches like forest or grassland). Agricultural expansion has resulted in the simplification of landscape pattern, primarily by the removal of natural and semi-natural patches (Robinson and Sutherland 2002), that provide an important source of habitat (e.g., forage and nesting sites) for many organisms, and a reduction in the types of crops produced often leading to the establishment of monocultures (Matson et al. 1997). As the proportional area covered by crop fields increases, crop fields are more likely to border other crop fields than non-crop covers. When suitable uncultivated habitat becomes reduced in size and distant from other similar patches, the resulting isolation

can affect populations (Fahrig 2003), for example, by decreasing accessibility to resources, foraging distance and duration increases especially for central place foragers (Osborne et al. 2008a). In fields where some proportion of semi-natural habitat remains, these patches may support fewer populations due to disturbances from nearby farming activities, including by chemical means (e.g., the off-target drift of agricultural chemicals). For organisms to establish and persist in agricultural areas, there must be sufficient availability of resources (i.e., variety in the classes of land covers and the habitat types they represent) (Fahrig et al. 2011).

How pollinators experience their habitat patches across the landscape is key to assessing the effect of landscape structure on pollinator populations. For pollinators, including bumble bees (*Bombus* sp.), the landscape consists of some habitats that provide floral (Kremen et al. 2019) and nesting resources, that vary in space and time. As such, the spatial distribution of pollinators should be linked to the availability of these habitats (e.g., the presence of plants they visit or nesting sites within natural or semi-natural patches in the landscape). Landscape structure has been shown to affect the abundance, diversity and demography of pollinators (Dieckötter et al. 2006, Crone and Williams 2016). Resource availability (e.g., in the composition and configuration of land covers) caused by land-use is also likely to affect pollinator nesting and foraging success (Osborne et al. 1991, Öckinger and Smith 2007, Carvell et al. 2011, Diaz-Forero et al. 2013).

Bumble bees are important pollinators of wildflowers and some commercial crops, including blueberry (Ratti et al. 2008, Tuell et al. 2014). These eusocial insects follow an annual colony cycle, where queens emerge from hibernation to establish colonies (Heinrich 1979). Queens and later sequential cohorts of workers collect pollen and nectar to provision the colony. Bumble bees require a constant supply of forage for colonies to survive and produce new sets of reproductives (i.e., queens and males) at the end of the season (Heinrich 1979, Goulson 2010). To maximize fitness in the absence of competition, bumble bee queens should choose nest sites in high-quality habitats that offer the best floral resources and the greatest foraging opportunities for workers. Wild bees experience the landscape at different spatial scales depending on their dispersal abilities influenced by their body size, where large-sized bees travel further than small sized ones (Greenleaf et al. 2007, Williams and Kremen 2007). As central place foragers, the location of a

nest relative to the distribution of floral resources determines foraging success, a likely correlate of reproductive success (Suzuki et al. 2009). When floral resources are nearer to nest sites, travel time and flight energy cost are reduced for foraging bumble bees. This creates the expectation that the profitability of floral resources should decrease as the spatial extent over which resources are available (i.e., the scale of resource availability) increases (Pyke 1984). Hence all else being equal, worker bees should prefer floral resources closer to the colony.

Landscape structure as inferred from patterns of land use can affect pollinator demography. Within crop fields, the abundance of mass-flowering crops is positively related to the growth of bumble bee colonies, but the effects on the production of reproductives are inconsistent (Westphal et al. 2009, Williams et al. 2012). In another study, bumble bee colony growth was negatively related to the abundance of mass-flowering orchards but positively correlated with the amount of semi-natural habitat (Proesmans et al. 2019). Other studies have shown that greater floral resources found in organic fields, as compared to conventional ones, increased colony success and individual worker condition in *Bombus impatiens* (Adhikari et al. 2019).

This thesis builds on the existing literature to examine the effect of the landscape structure on bumble bee demography, adding consideration of the spatial scale at which bees respond to the landscape. Nest boxes, naturally occupied by bumble bees, were placed in an agricultural landscape comprised of a mosaic of suburban cover, conventional agriculture dominated by commercial berry crops and semi-natural land covers to measure the demographic response of bumble bees. To my knowledge, this is the first study that examines the effect of the landscape on nest founding of wild bumble bees and its scales. I also extend the literature on how the landscape affects colony success of bumble bees.

A summary of bumble bee lifecycle and biological details of my study system needs to be understood to inform the hypotheses and predictions. Bumble bee queens after mating, forage to build up energy reserves and prepare for hibernation. An inseminated queen locates a suitable area or excavates a site where she will hibernate throughout the winter until the average temperature increases to about 5- 25°C (Heinrich 1979). When temperatures are warm enough, the queen emerges from hibernation to commence

nesting. The queen first forages on nectar for herself and then begins to search for a suitable nesting site, where the colony will be established (Heinrich 1979). The search process involves landing on the ground at frequent intervals, crawling under leaves and investigating holes in the ground and if a suitable nesting site is not found the queen resumes her wandering flight. Search can last all day, can go on for days up to about two weeks or more, until she finds a suitable site i.e., a dark cavity or within a clump of decaying grass on the surface of the ground or an abandoned nest of a rodent. Old rodent dens are preferred sites for many ground-nesting bumble bee species because rodent nests contain insulating material which bumble bees repurpose for the insulation of their colony. Once a nest site is selected, a bumble bee queen forages for nectar which she deposits into a honey pot fashioned out of waxy scales exuded from glands on her abdomen. She also forages on pollen from which she creates pollen clumps, and on which she lays a batch of 8-10 eggs. The queen incubates the eggs until they hatch into the first instar and provisions the larva as they pupate and finally emerge as adults. After the first workers emerge, they take over the duties of foraging and caring for the subsequent brood. The colony then continues to grow in its brood size and its honey and pollen stores. At some point in the colony cycle, the colony switches from the production of workers to the production of reproductives (i.e., males and queens). The males and new queens leave the nest to mate where the mated queens will repeat the colony cycle. At the end of the season, the old queen dies, the nest senesces, leaving new queens to go through the winter. Those that survive begin the colony cycle anew.

In the early stages of colony growth during nest founding, semi-natural land covers are the main sources of flowering resources for wild bumble bees. Later in mid-spring, the landscape with mass-flowering berry crops experiences a pulse in flowering resources from which bumble bees forage, in addition to those provided by semi-natural habitat (Winston and Graf 1982, MacKenzie and Winston 1984). Mass-flowering berry crops provide a significant amount of forage for bees, however, this forage only lasts for about 3 weeks in a given field. In the absence of mass-flowering berry crops, wild bumble bees must rely on forage provided by natural habitat to complete their life cycle.

In this thesis, I addressed the following questions: (1) What effect does the landscape structure (i.e., the composition and configuration of land covers) have on nest founding and colony success? and, (2) Which spatial scale, or scales, best explain the response of bumble bee colonies to landscape structure? To answer these questions, I test the following hypotheses and predictions about how the landscape structure potentially affects nest founding and colony success of bumble bees:

H1. Landscapes with semi-natural land covers have more nesting sites for bees, increasing the chances of nest founding. These landscapes also increase the probability of colony success because of more foraging opportunities. This leads to the following two predictions that I will test. More semi-natural habitat will be associated with more evidence of nest founding (P1a) and with higher colony success (P1b).

H2. Landscapes that have “beneficial agricultural” (i.e., commercial berry crops) cover are likely to have fewer nesting sites and fewer in-field wildflowers due to on-farm activities such as mowing and application of pesticides. However, “beneficial agriculture” fields have rich floral resources that are available after the period of nest formation and early to mid in the period of exponential growth of colony size, whereby these rich floral resources can boost colony performance (Figure 1). The intensiveness of commercial berry agriculture through on-farm management and inputs such as mowing and pesticide application results in habitat disturbances which can decrease nesting and in-field wildflowers, and therefore should decrease the chances of nest founding (H2a). Also, a mismatch between the period of maximal floral resource availability, provided by berry crops, and the period of nest founding, may further reduce the chances of attracting queens to found nests (Figure 1). Finally, the success of colonies that establish in the presence of a large amount of “beneficial agriculture” is (i) likely to be low at the early stage of colony growth (the three to four weeks of queen only foraging, before workers have emerged), due to the absence of in-field floral resources when berry crops are not in bloom (ii) likely to be high at mid-stage of growth in colony size (when workers have emerged, but the colony is not at the reproductive stage), due to the copious and beneficial floral resources provided by the crops (iii) likely to be low at the late stage of colony growth

(during the production of reproductives), due to the absence of floral resources when berry crops are out of bloom, coupled with less in-field season-long wildflowers (H2b). As such, few nests should be founded (P2a) at sites with more commercial “beneficial agriculture” and colony success should be (P2bi) low at the stage of colony growth, (P2bii) high at mid-stage of growth in colony size and (P2biii) low at the late stage of colony growth.

H3. The suburban landscape, with moderate to low-intensity infrastructural development, is likely to provide floral and nesting resources due to the presence of suburban parks and gardens, home gardens and other undeveloped open spaces (Goulson et al. 2002). Gardens and parks represent a potentially rich source of diverse and abundant floral sources and also, may contain nesting material such as leaves, artificial structures and decaying tree stump (Fetridge et al. 2008). On the other hand, roads, building and paving’s which are also present in the suburban landscape are non-habitat for bees and unlikely to attract bees. Therefore, suburban land covers with less hardscape (i.e., roads, buildings etc) and more open spaces, flower-rich gardens and parks should support nest founding and colony success. Hence nest founding (P3a) and colony success (P3b) should be positively associated with the amount of suburban cover in the landscape.

H4. Edge habitats (i.e., the narrow transition zone between different cover classes) can supply foraging resources through their ability to support diverse plant communities that would not be abundant within either adjacent land cover types (Del Barrio et al. 2006). If flowers and nesting resources are abundant because edges are undisturbed, this should increase the chances of nest founding and increase colony success. Hence more nests should be founded (P4a) with higher colony success (P4b) at sites where there are more edges representing more adjacencies between land cover classes.

H5. Nest searching bumble bee queens after emerging from hibernation actively sample the landscape in search for potential nesting habitat (Hagen et al. 2011, Makinson et al. 2019). Queens search broadly to

find the best nesting places hence nest founding should be better explained by the landscape measured at a small spatial scale (H5a) (e.g., 250 m) because searching broadly sharpens the queen's ability to make precise choices about the best nesting location (P5a). Alternatively, queens have a large body size (relative to workers), and this allows them to forage and explore their landscape up to several kilometres from their nest sites (Greenleaf et al. 2007). If nest sites are rare in the landscape, bumble bee queens are sometimes unable to nest close to the best sites. As such, a queen should accept a nest site further from the best nesting locations and therefore, she experiences a big landscape afforded by her large body size (H5b). Central-place foraging of large-bodied bees, therefore, predicts a large scale for queens following nest establishment based on their body size (P5b).

H6. Bumble bee queens forage at least three to four weeks during the period of exponential growth of the colony (queen only foraging, before workers have emerged) as such, contribute to the outcome of colony success (Heinrich 1979). Therefore, the landscape for colony success during the period of queen only foraging depends on the outcome of H5, i.e., the landscape is small if nest searching by queens' matters (H5a) and the landscape is big if queen body size matters (H5b). Workers, on the other hand, do the bulk of the foraging until the final stage of the colony cycle (production of reproductives), therefore workers (relative to queens) have a higher contribution to the outcome of colony success. Foraging bumble bee workers, unlike queens, have a small body size and therefore the expectation of small foraging distances (Greenleaf et al. 2007). On average, bumble bee workers forage less than 1 km from the nest (Walther-Hellwig and Frankl 2000, Wolf and Moritz 2011). Bumble bee workers should preferentially forage on flowering plants in habitats that are closer to their nest because the travel cost of foraging increases as they move further away from their nest (Osborne et al. 2008a). Hence colony success should be better explained by the landscape measured at a small spatial scale (i.e., < 1 km) (P6).

METHODOLOGY

Field sites

The study was conducted in the Lower Mainland of British Columbia, Canada. The study area is a mosaic of intensive agriculture, suburban and semi-natural habitats which together provide variation in land covers (Table 1) suitable for testing the hypotheses. I selected twenty-seven sites that represented a range of landscapes, based on land cover compositions (i.e., class and proportional areas of surrounding land covers) that could potentially provide resources for wild pollinators (Figure 2). To optimize the independence and amount of data collected from these sites (i.e., to reduce spatial autocorrelation in statistical models) study locations were at least 2 km apart. A 2 km separation makes it unlikely that individual foraging bees from adjacent sites could forage from the same patches, given that most bumble bee workers forage less than 1.5 km from their colony (Walther-Hellwig and Frankl 2000, Redhead et al. 2016).

Bumble bees

At each site in 2019, 10 underground bumble bee nest boxes were installed, spaced roughly 2 m apart. Boxes were installed on the sloping banks of roadside ditches about 5 m from a highbush blueberry farm, or, on available slopes on uncultivated space near the farm when ditch banks were not available (Figure 6a). The boxes were 15 cm x 18 cm x 19 cm cubes (external dimension) made from untreated wood with entrance holes 2.5 cm in diameter (Figure 6b). The interior of each box was lined with upholsterers' cotton for insulation and to provide a substrate for nest establishment (Hobbs et al. 1960). The boxes were buried about 22 cm below the surface of the ground. A PVC tube 1.8 cm in inside diameter and 20 cm in length was fitted to each box to serve as an entrance and exit route for bees (Figure 6c). The top of each box was covered with a plastic sheet to prevent water from entering the box from above. During excavations, sod was removed so that it could be placed back on top of the boxes. V-shaped excavations

leading to the entrance of the PVC tubes were made, with the expectation that nest searching bumble bee queens would follow the excavation walls into the entrance of the nest (Figure 6d).

Boxes were installed in early March before the emergence of over-wintering queens and were retrieved in late July when most of natural bumble bee nests in the Lower Mainland begin to senesce (personal observation). Most boxes collected at this period were in the final stages of the colony cycle, as such, colony remnants were mostly intact and not yet decomposed by mould, insects, or rodents. Colony remnants that were in a state of decay were those that had failed either at the beginning or the middle of the season (mid-March to mid-May). I recorded a box as occupied if there were signs of bee activity or colony remnants. The contents of all occupied boxes were removed and stored in a freezer at -20 °C to preserve colony remnants from further decay and for later lab analysis. I dissected all colony remnants retrieved from nest boxes and counted eggs, pupae, larvae, emerged cells (waxy or silky structures that remain after pupal emergence), honey and pollen pots, and workers using Alford (1970) to distinguish stages. I was unable to distinguish workers and reproductives (i.e., queens and males) based on size and so all adults were counted as “workers”. Colony weight was the wet weight of colony remnants (i.e., brood, honey, and pollen pots) plus adult bees (workers). The above metrics collectively were used as a measure of colony success. What matters most for a colony to be deemed as successful is (1) final size (i.e., food stored, brood produced (larvae, eggs, pupae), weight gained, brood structures built) and (2) fitness; their ability to produce reproductives (new queens and males). I approximated colony success using the number of each brood stage and the number of adults as a metric of reproduction.

Landscape

The landscape for each sampling location was quantified using raster imagery from the Agriculture and Agri-Food Canada (AAFC) 2019 annual crop inventory data at a spatial resolution of 30 m (Annual Space-Based Crop Inventory for Canada 2019). The raster imagery (classified into land cover classes) was already examined for accuracy of land cover classification by the provider, where crop and non-crop cover accuracies were 89.35 % and 76.39% respectively. I further confirmed these classifications using a

combination of on-site inspection in the neighbourhood of my sites and manual confirmation using Google Earth satellite imagery. From its original ~ 45 cover type classification, the raster imagery was reclassified by clustering classes into three groups: semi-natural cover (forest, shrubland, pasture, grassland, and wetlands), beneficial agricultural cover (blueberry, raspberry, and cranberry fields) and suburban cover (residential, built-up areas and underdeveloped open spaces) (Table 1). The reclassifications were based on an understanding of the resource requirements of bumble bees where I grouped cover types based on an expectation that they would or would not contain foraging or nesting resources. Semi-natural covers were those land cover likely to provide floral resources and suitable nesting sites for bumble bees during the colony cycle (Holland et al. 2017, Proesmans et al. 2019). Semi-natural land cover is thus defined as those habitats/land covers that are within the category of non-crop land cover (i.e., habitats that retain some natural features including vegetation and have not been extensively modified by humans). The “beneficial agriculture” class was defined to include commercial berry crops as primary contributors to this class with cranberry and potato making up the rest (Table 1). Individual fields provide a pulse of floral resources in mid-spring just after overwintering bumble bee queens have emerged, with floral bloom lasting for about three weeks in a given field and about five-six weeks for all fields in the landscape (Button and Elle 2014). Suburban cover included residential homes, built-up areas and medium to low-intensity infrastructural development. It can contain a mixture of resource habitats because these areas include home and community gardens, suburban parks that may provide floral resources (Baldock et al. 2019) and non-resource habitats such as suburban roads, buildings, and paving’s which are non-habitat for bees and do not provide nesting or floral resources.

Landscape metrics considered in this study were related to both composition (land cover types and their proportions) and configuration (spatial arrangements of cover types). I computed landscape composition as (1) the proportion of semi-natural land covers; (2) the proportion of beneficial agriculture covers; and (3) the proportion of suburban land covers. Landscape configuration was measured using edge density of land cover classes, calculated using the ‘landscapemetrics’ package in R (Hesselbarth et al. 2019, R Core Team 2019). Edge density is a measure of the total length of edge in the landscape for a given area

of cover type and reflects the adjacencies of land cover types. It is calculated as the sum of length (m) of all edges of a land cover type, divided by total landscape area (m^2) (McGarigal and Marks 1995). Edge density can be used to infer the existence of edges from the proximity of two land cover classes (Ma et al. 2013) and can be a useful measure of landscape configuration, because, it can be related to processes such as habitat complementation (i.e., improved outcomes for organisms that need resources provided by two adjacent land cover types). While the edge metric is a property of a landscape and not itself a land cover, it can be used to infer the existence of “edge habitat” not evident on a land cover map. In the study area, edges between land covers are often themselves a distinctive habitat type. For example, banked ditches or verges can typically be found between crop and non-crop cover. Other edge habitats between cover types include grassy margins with herbaceous vegetation, remnant and planted hedgerows, as well as weeds that may provide forage for bees (E-Flora BC: Electronic Atlas of the Flora of British Columbia 2021). Therefore, edge density can conceivably be used as an index of the availability of floral resources for bumble bees as well as suitable nesting substrates likely to be found in these transitional land covers (Clausen 2017). In this study, I employed a generalised classification of habitat edges where, edges could be habitats found within cropland covers, or habitats between non-crop and cropland covers (Table 2, Figure 3). Primarily, edge habitat in this study constitutes the interface/transitional habitat between land cover classes, for example, interface between suburban-coniferous forest, coniferous forest-broadleaf forest, urban-pasture, urban-blueberry cover, and urban-broadleaf forest (Figure 4). The “get_adjacencies” code in the ‘landscapemetrics’ package in R was used to generate a matrix of cell adjacencies that represents the interface between land cover classes (Hesselbarth et al. 2019). The transitional habitat as the interface between land cover classes presented in Figure 4 can be categorized as margins that can contain floral and nesting resources when they are undisturbed, or margins resulting from changes in the constituents in one of the two land cover classes, that presents conditions necessary to boost floral communities.

The proportion of land cover type and edge density were calculated within six spatial scales defined as circular rings of 0-250 m, 0-500 m, 0-750 m, 0-1500 m, 0-2000 m, 0-2500 m radii around each site, where the site location was the centre of an array of ten nest boxes (Figure 5). The spatial scales were

chosen to reflect a range of distances up to the maximum typical foraging distance of worker bumble bees (Osborne et al. 1999, Wolf and Moritz 2011, Rao et al. 2019). Most studies examining the spatial scale at which bumble bees perceive and interact with the landscape use circular rings at multiple distances from a focal sampling location (Steffan-Dewenter et al. 2002, Westphal et al. 2003), and for comparative purposes, the same strategy is adopted here. Landscape variables (i.e., composition) were computed using tabulate area tool in ArcGIS (ESRI 2011).

Data analysis

Boxes that showed signs of bee activity were classified as occupied (1) while those that did not were deemed unoccupied (0). Only boxes that were available for potential occupation (i.e., boxes in which the entrances were not covered by debris, (n=106) were used in this analysis. For the analysis of nest founding, I used data from twenty-seven sites (n=27) containing a total of 106 occupied and unoccupied boxes. For the analysis of colony success, I used data from twenty-three sites (n=23) where the number of occupied boxes summed to 63.

Principal Component Analysis (PCA) was used to reduce the collective metrics of colony success to a single index of colony success (i.e., by using scores on the first principal component axis comprising the largest amount of variance in these metrics) (Table 3). PCA uses a correlation matrix to represent the relationships among variables, and the correlation coefficient assumes normality of variables. Metrics of colony success were first transformed using the Box-Cox transformation to approximate normality (Table 3). Where appropriate, a constant was added to the individual colony success metric to ensure positive values before power transformation (Table 3).

I used mixed-effect multiple regression models to test the effect of the landscape structure on nest founding and colony success of bumble bees. For the analysis of nest founding, I used a binomial distribution with a logit link function. For the analysis of colony success, I used a Gaussian distribution and an identity link function. For both response variables, six models were fitted each corresponding to

landscape variables measured at each of the spatial scales from 250 m to 2500 m radius around sampling locations. Models included the proportion of semi-natural land cover, the proportion of beneficial agricultural land cover, the proportion of suburban land cover and edge density. Multicollinearity among landscape variables was assessed using the variance inflation factor (VIF) (Fox and Monette 1992). Variables with VIF that is greater than ten are considered collinear and should not be included in the same model. For all variables in all models, VIF was less than ten. Site identity was included as a random effect in each model (i.e., a different intercept was fitted for each site). All models initially included a two-way interaction term between beneficial agriculture and edge density however, non-significant interactions were removed to decrease model degrees of freedom. All predictor were standardized by subtracting the means from each value and dividing by the standard deviation. Standardization ensures coefficients (and therefore effect sizes) are comparable for variables measured on and at different scales.

To determine the spatial scale that best explains the effect of the landscape structure on nest founding and colony success, I compared models fitted at each spatial scale (250 m to 2500 m). I used the corrected Akaike Information Criterion (AIC_C) for a small sample size to compare fitted models. The delta AIC_C (ΔAIC_C) is the difference in AIC_C between the best model and the model being compared. A model with a ΔAIC_C value of zero is considered the best model. When the difference between the best model (i.e., $\Delta AIC_C = 0$) and a given model is lower than 4 ΔAIC_C units, the given model has comparable explanatory power to the best model, however, when the difference is greater than 4 ΔAIC_C units, the given model is not considered part of the best models and can be excluded (Burnham et al. 2011). I selected the model with the lowest delta AIC_C value and the highest model weight as the best model among the list of compared models (Anderson and Burnham 2004). I used the lme4 package to fit all regression models. All statistical analyses were conducted in R (R Core Team 2019).

RESULTS

Nest founding.

Overall, 63 of 106 boxes had bee colonies formed in them. This represents a 59 % founding rate of bee boxes across all sites.

The chances of nest founding decreased at sites with more beneficial agriculture cover (Table 4), supporting the hypothesis that surroundings with more beneficial agriculture cover will decrease nest founding (H2a). The observed effect of beneficial agriculture cover was at 750 m, 1500 m and 2000 m spatial scales, peaking at 750 m (Figure 7). Peaks are inferred from the largest parameter estimate for that variable from models at all spatial scales. The proportion of suburban cover decreased the chances of nest founding (Table 4), rejecting the hypothesis that landscape with more suburban cover will increase nest founding (H3). The negative effect of the suburban cover was observed at spatial scales greater than 1500 m, peaking at 2500 m (Figure 8). Nest boxes were more likely to be occupied at sites with more edge density (Table 4), supporting the hypothesis that higher edge density will increase nest founding (H4). The effect of edge density on nest founding was observed at all spatial scales, peaking at 1500 m (Figure 9). The proportion of semi-natural habitat had no significant relationship with nest founding (Table 4), rejecting the hypothesis that surroundings with more semi-natural habitat will increase nest founding (H1). Semi-natural habitat had no significant relationship at any spatial scale (Table 4).

Colony success.

The PCA results show that the first two components accounted for 76.8 % of the variance in the original dataset. The first principal component explains 61.3 % of the variance and was used as a measure of colony success (Table 3). Using PC1 as a measure of colony success, semi-natural habitat, edge density, the suburban land cover and beneficial agriculture cover individually and collectively did not explain colony success (Table 5).

Spatial scale of response.

The landscape measured within a 1500 m radius best-explained nest founding and supporting the hypothesis that bumble bee queens will have a large scale based on their large body size and rejecting the small-scale-from-sampling hypothesis (H5a) (Table 6). However, colony success was unexplained by the landscape at any spatial scale (H6) as the null model was the best fit (Table 7).

DISCUSSION

Effect of the landscape on nest founding and colony success.

I found no support for a relationship between the proportion of semi-natural habitat with either nest founding or colony success. These results are contrary to the hypothesis that semi-natural habitat will increase nest founding and increase colony success (H1), and to other related studies that have found positive relationships between the amount of semi-natural habitat and the success of nearby bumble bee colonies (Spiesman et al. 2017, Proesmans et al. 2019). Traits of land cover types have previously been associated with measures of wild pollinator abundance (Bartual et al. 2019). I did not measure the spatial and temporal availability of floral and nesting resources within any habitat in this study. Measuring resource availability would have better described the quality of the landscape and its potential to sustain bee populations and would have been a finer-scale metric in assessing the value of the landscape for pollinators, than the coarse land cover classification I used (Roulston and Goodell 2011). In addition to quality, the area of a land cover class is also an approximation of the amount of habitat. Without these additional details, I can only speculate about whether the lack of support for the predicted relationship between semi-natural habitat and colony founding and success is a causal one or rather due to the insufficiency of the approach used for measuring habitat availability. Coniferous forest, broadleaf forest and pasture make up about 90% of semi-natural habitat while shrublands, mixed wood forest and wetlands make up most of the rest (Table 1). Even though these habitats would have provided the bulk of non-crop floral resources and nest sites,

there remains the possibility that other land cover types not considered in this study could have been good for bumble bees. Pollinators visiting semi-natural habitats may have been attracted to alternative foraging and nesting opportunities elsewhere, for example, in nearby edge habitats or ditches. In other words, the importance of floral and nesting resources in semi-natural habitats for bumble bees may have decreased as local availability of alternative food and nest sites elsewhere increased, reflecting the results.

Bumble bees forage a few kilometres beyond the neighbourhood of their nest, allowing their exploration and use of floral and nesting resources within habitat types in the landscape (Osborne et al. 2008a). Also, their generalised use of flowering plants allows bumble bees to forage widely, permitting their use of many types of flowers that are available (Svensson et al. 2000, Kells and Goulson 2003). This may further explain why semi-natural habitats were not important in this study, because bumble bees could have encountered other profitable habitats.

The chances of nest founding decreased at sites with more beneficial agricultural land covers supporting the hypothesis that landscapes with a large amount of beneficial agriculture will decrease nest founding (H2a). The availability of abundant early season floral resources allows queens to establish nests and produce workers who gather more food for the colony (Rundlöf et al. 2014). Beneficial agriculture, in my study landscape, consisted primarily of commercial mass flowering blueberry, raspberry and cranberry crops which together make up a large crop cover of the study area (Annual Space-Based Crop Inventory for Canada 2019). Sites near mass-flowering berry crops usually have few nesting sites and few alternative season-long forage for bumble bees due to intensive on-farm practices and inputs, however, these crops produce huge quantities of floral resources that bumble bee colonies can benefit from, although the flowers are available for a short period, followed by a reduction in floral resources after bloom (Persson and Smith 2013). Such a large pulse in forage does not usually coincide with early nest initiation and may result in a phenological mismatch between resource availability and timing of nest founding. For example, in my study location, the bloom of commercial blueberry crops begins in late April or early May depending on the temperature, and last for about five to six weeks (MacKenzie 1997, Button and Elle 2014). In contrast,

some species of bumble bee queens emerge in early to mid-March, and through April while, others emerge in June, during which nest searching and colony establishment commence, but neither case (March and June) is likely to overlap with the mass-flowering pulse of berry crops (Ratti et al. 2008, Lanterman et al. 2019).

Some of the most common bumble bee species from earlier surveys of semi-natural habitats and berry crop fields in my study area are reported by MacKenzie and Winston (1984) and Ratti et al. (2008). Information on the timing of emergence of bumble bee queens specific to my study area is mostly unavailable, however, based on the timing of emergence of similar bumble bee species elsewhere, and knowledge of weather conditions that trigger bumble bee queen emergence, and a comparison of the period onset of those weather condition relative to my study region, it is possible to estimate the timing of bumble bee queen emergence in my study area e.g., as done elsewhere by (Koch et al. 2012). I estimate the period of the emergence of bumble bee queens as starting from March to July with early emerging queens being prevalent. The timing of queen emergence and bloom of berry crops may result in a mismatch where queens of early-emerging species (March emerging queens) have limited access to floral resources because mass-flowering berry crops are not yet in bloom. Fewer nest sites and alternative season-long in-field wildflowers and phenological gaps during which little to no forage resources are available for bumble bees when they are nest searching may not attract bumble bee queens to nest at sites with “beneficial agriculture” and may explain why the chances of nest founding decreased with the proportion of beneficial agriculture in this study. Surroundings dominated by mass-flowering commercial berry crops, therefore, may not provide adequate forage for pollinators who require an adequate supply of early-season forage to initiate the colony.

The proportion of suburban cover decreased the chances of nest founding, contrary to the hypothesis that the suburban landscape can provide floral resources and nesting sites as such will increase nest founding (H3). Results from previous studies show contrasting results with this study on the response of bumble bee colonies to the urban/suburban landscape. For example, Goulson et al. (2002) found that bumble bee colonies gained weight more quickly and attained larger sizes when placed in a suburban garden

than when in farmed land. Similarly, Samuelson et al. (2018) found that bumble bee colonies placed in village and city locations had higher reproductive success and had higher worker numbers than those placed in conventional agricultural locations, likely because of the availability of diverse floral resources in urban areas than in conventional farms.

While I did not measure floral resources in the suburban landscape in this study, I only assumed the value of the suburban cover for pollinators based on the numerous studies that have found the suburban and urban landscapes support wild bee pollinators (Fetridge et al. 2008, Matteson et al. 2008, Banaszak-Cibicka and Żmihorski 2012). However, since no two landscapes are the same and the value of a suburban cover for bee can vary depending on the local circumstance of the landscape (Winfrey et al. 2009), with the cost and benefit of the suburban cover dependent on factors such as they type and intensity of infrastructural development, amount of surrounding natural and semi-natural habitat and the availability of floral and nesting resources. The local circumstance of the suburban landscape in my study area may not have been ideal to support wild pollinators. Even though the suburban landscape in my study area featured medium to low-intensity development, such development could still pose challenges for wild native pollinators. Impervious features like roads, paving and buildings which are characteristics of the suburban landscape in my study location are non-habitats for pollinators (Geslin et al. 2016). I speculate that because of the nature of impervious features as hardscapes with degraded areas and of dry and compacted soils, they generally support few foraging and nesting opportunities (Cane et al. 2006). Suburban cover may have affected bumble bees through impervious features like roads, buildings, pavements, and lawn focused vegetation which may have affected resource availability by reducing resources for nest founding queens (McIntyre 2000). Without high-quality nesting habitat, the suburban landscape is unlikely to support nest searching bumble bee queens (Xie et al. 2013). In the suburban landscape, home gardens, lawns or suburban parks can provide flowering and nesting resources (Baldock et al. 2019) all things being equal. However, the floral resources from homes and parks can be of low quality because perhaps, homeowners and landscapers may not be purchasing the right plant species for pollinators, or may prefer to plant ornamental plants for their aesthetic value and less of their pollen and nectar for pollinators (Garbuzov and Ratnieks 2014).

Campbell et al. (2017) showed that 49 % of homeowners chose pollinator-friendly plants because of their attractiveness and not necessarily for the benefit they provide for wild pollinators. When floral resources are either lacking and/or of low quality in suburban landscapes, bumble bees would have to seek foraging opportunities elsewhere making the suburban landscape unattractive for pollinators. Given that the suburban landscape in my study location includes impervious features which are non-habitats, coupled with the possibility of low-quality flowers from homes and gardens, it is likely that suburban landscape in my study may have supported fewer resources, therefore, making it unattractive for bumble bee queens, and might explain why the chances of nest founding decreased with the proportion of suburban cover in this study.

The chances of nest founding increased at sites with more edge habitat which is quantified using the edge density metric and in support of the hypothesis that landscape with edge habitats will increase nest founding (H4). Edges, as narrow zones of transition between different land covers, may represent environmental conditions necessary to support a range of plant communities and their associated fauna (Marshall 2004). Plant species compositions and species numbers have been found to be higher in edges than in adjacent cover, particularly in margins and verge within extensively managed agricultural landscapes (Auestad et al. 1999, Hald 2002). Smith et al. (1993) found that uncultivated field margins allowed to naturally re-vegetate had woody perennials and many colonial plant species establishing first, with an accelerated transition from annual to perennial dominated flora. Flower rich edge habitats are important in conserving many threatened arthropods including wild bee pollinators (Noordijk et al. 2009). *Bombus pauloensis* queens preferred to established nest mostly at the edges of forest plantations, which had greater floral diversity and perhaps provided colony workers with good foraging opportunities (Cavigliasso et al. 2020).

In my study region, banked ditches or verges, grassy margins with herbaceous vegetation, remnant and planted hedgerows, as well as weeds are habitats and represent edges as transition zones typically found within crop cover and between crop and non-crop cover. Because these areas tend to be relatively

unmanaged (i.e., fewer disturbances of soil substrate (personal observation)), or are edge habitats resulting from changes in the constituents in one of the two land cover classes, that presents conditions necessary to boost floral communities, they may retain some features resembling semi-natural habitat, that enables them to support plant species of greater floral diversity (Herzon and Helenius 2008). This, in turn, may provide forage and nesting habitat for pollinators (Lagerlöf et al. 1992, Marshall and Moonen 2002). Edge habitats in the study locations may have provided forage in early spring and were favoured as high-quality nesting habitat by nest searching queens. The dominant crop in my study region is commercial blueberry crops (Annual Space-Based Crop Inventory for Canada 2019) which bloom after most bumble bee queens have emerged from hibernation to found nests. While flowers from crops are unavailable in early spring, emerged bumble bee queens can benefit from complementary forage and nest sites provided by edge habitats. As such the increased chances of nest founding at sites with higher edge density in this study reflect the hypothesis.

In general, landscape did not explain the success of bumble bee colonies. This result is surprising because I expected a directional relationship between colony success and the landscape. Recall that I did not measure the spatial and temporal availability of floral resources within any habitat in my study landscape and that a measure of floral resources availability would have been better at assessing the quality of the landscape. Because I presumed resource availability using the area of land cover class, it is challenging to disentangle whether the landscape not explaining colony success is because the area of a habitat is a poor proxy of resource availability, or due to the insufficiencies in the approach used for assuming habitat and resource availability. The amount of a habitat type can be a good variable in explaining bee abundance, as studies have found positive correlations between bee abundance and diversity and area of natural habitat in the landscape (Steffan-Dewenter 2003, Bennett and Isaacs 2014), however, wild bees including bumble bees do not necessarily respond to the amount of cover class in itself, they respond to, for example, the abundance and the distribution of floral resources within land covers in the landscape (Potts et al. 2003). Using the amount of a cover class as an approximation for resource availability can be

useful in certain circumstances, however, the amount of a cover class may not necessarily reflect resources in that land cover or even resource distribution. Colony growth and reproduction increased with floral diversity but decreased with site area and proportion of forest (Lanterman and Goodell 2018). In low flower dominance locations, the amount of natural habitat decreased colony growth, however, when flower dominance was high, the amount of natural habitat did not influence growth (Spiesman et al. 2017), suggesting that bumble bee colony growth depends on factors related to resource availability (Williams et al. 2012, Crone and Williams 2016).

For bumble bees, it may be possible that their preferred plant species may be associated with a patch in a habitat type, as such, it does not matter how much of that habitat is available, what matters most is the patch the contains their most preferred forage. Because bumble bee workers are mobile organisms and are flexible in the distance to which they will forage for food, what matters is resource availability and how accessible they are (Jha and Kremen 2013a). If by chance a bee's response to resources in a habitat type has no direct link to the amount of that habitat type or there is flexibility in a bee's use of resources in the landscape such that the amount of habitat and configuration of habitat types do not matter, then it is expected that cover/habitat amount and configuration as variables will not explain colony success. It is likely that other features of the general landscape that are unmeasured in this study, might explain colony success based on how bumble bees respond to the landscape. Further studies may require the inclusion of detailed landscape measurements such as the abundance and diversity of floral resources to potentially explain colony success.

Spatial scale of response.

For pollinators, spatial scale has been linked to species body size which influences species foraging ranges and flight distances (Steffan-Dewenter et al. 2002). I found that landscape variables measured at 1500 m best explained nest founding. There is evidence to suggest bumble bee queens disperse and establish colonies many kilometres away from the queen's natal nest site (Hagen et al. 2011). Using genetic relatedness of bumble bee workers and queens, Lepais et al. (2010) found that new queens disperse at least

3-5 km away from their natal nest to establish their own nest. Jha and Kremen (2013b) found that in urban environments, *Bombus vosnesenskii* queens dispersed and preferred to nest within 1-9 km spatial scale of their natal colonies, likely influenced by habitat alteration within the urban landscape. In my study area, land cover measurements increased with spatial scale. If so, then I assume that the amount of land cover should be proportional such that the large spatial scale should provide the highest resolution of information on the distribution, quality, and quantity of resources in the landscape, leading to the selection of the most suitable habitat. An outcome is that, as bumble bee queens explore the landscape, the probability of encountering forage and nesting habitats increases leading to the selection of the best nesting location and therefore a queen experiencing a small landscape. However, this idea was unsupported in the present study but there was support for the body size hypothesis. Bumble bee queens have a large body size as such the expectation of a large flight distance afforded by her large body (Greenleaf et al. 2007). When nest sites are rare in relation to foraging sites, bumble bee queens are sometimes unable to nest close to the best sites as such a queen should accept a nest site further from the best nesting locations and therefore, she experiences a big landscape afforded by her larger body size. Nest founding relating most strongly to variables measured at the 1500 m scale may suggest bumble bee queens experience the landscape at a large spatial scale where they may be selecting the most readily available nesting habitats they find.

There was no response of colony success to the landscape measured at any radius from the colony. From the results, no individual model on colony success mattered and therefore spatial scale will not matter in that regard. This result speaks to the earlier suggestion that there may have just been a poor link between measures of the landscape structure and colony success.

CONCLUSIONS

The proportion of beneficial agriculture decreased the chances of nest founding. This may be caused by reduced floral and nesting resources in areas of beneficial agriculture and a mismatch between the time of floral resources availability and initiation of nest founding, whereby, most queens found nests before berry crops are in bloom. The chances of nest founding increased at sites with more habitat edges quantified using the edge density metric. Edges may provide complementary floral and nesting resources, increasing their value, and likely attracting more nest searching bumble bee queens to nest in them. No relationship was found between semi-natural habitat and either nest founding or colony success, suggesting there is no evidence that forests, grasslands, pastures and wetlands, the principal semi-natural habitat in the Lower Mainland, may collectively be insufficient to provide nesting and floral resources for bumble bees. Perhaps other habitats provided food and nesting resources resulting in bumble bees foraging and nesting elsewhere. The chances of nest founding decreased with the proportion of suburban cover possibly due to reduced nesting and foraging habitat because of impervious features like roads, buildings and paving's or as a result of low-quality floral resources within the suburban landscape. Nest founding was best explained by the landscape at 1500 m spatial scale suggesting queens experience the landscape at a large spatial scale, where they may be selecting nesting habitats readily available to them. In general, colony success was not explained by the landscape even when measured at any spatial scale, reflecting a weak link between the measures of landscape structure used in this study and colony success.

The findings from the present study suggest commercial beneficial agriculture and suburban cover had negative consequences for nest founding in wild bumble bees within my study landscape. One of the main challenges in an intensive use agroecosystem like my study landscape is the availability of alternative forage sources for wild bees before, during and after the bloom of commercial berry and other mass-flowering crops (Nicholls and Altieri 2013). With land in high demand for crop cultivation, few uncultivated spaces remain resulting in fewer habitats for bumble bees. A lack of season-long food can result in the decline of wild pollinators and especially for bumble bee queens that are sensitive to the supply of food during early spring when they are founding nests (Suzuki et al. 2009).

Findings from the present study suggest that edge habitats seem to attract bumble bee queens to nest. This result reiterates the importance of edge habitats and confirms the general understanding that edge habitats provide complementary invaluable habitat sources for wild bumble bees in agricultural landscapes. Therefore, strategies aimed at conserving bumble bees within my study landscape may consider edge habitats as candidate locations for habitat focused conservation measures to preserve wild pollinators.

CHAPTER 3

GENERAL CONCLUSIONS

This research offers an insight into the demographic response of bumble bees to the landscape in an agroecosystem. I assessed how landscape composition in the form of the proportion of semi-natural habitat, suburban cover, beneficial agriculture cover, and configuration measured as edge density influenced nest founding and success of individual bumble bee colonies and the relevant spatial scale at which colonies responded to the landscape. Unlike other studies which have deployed nest boxes with managed and already fed pollinators, my research is first to my knowledge that assesses how the landscape in an agroecosystem affects the demography of bumble bees, by using nest boxes that are naturally colonized, representing a direct approach for estimating the fitness-related correlates of landscape conditions.

Semi-natural habitats did not influence colony founding and success. I interpret this result with caution since I was unable to measure floral and nesting resources availability. Also, the result is quite surprising as it does not fit the general narrative of semi-natural habitat as being an important source of food for bees in a resource-poor agricultural environment. This result may imply alternative use of floral and nesting resources provided by habitats other than semi-natural habitats. I speculate bumble bees may be adopting a jack-of-all-trades approach in resource utilisation by using available resources (i.e., food and nesting habitat) in the landscape irrespective of the type of habitats they are found in, therefore, maximizing resource acquisition in the landscape (MacArthur and Pianka 1966).

The chances of nest founding decreased at sites with more beneficial agriculture cover likely reflecting fewer floral and nesting resources and a mismatch between resource availability and nest founding. In my study area, beneficial agriculture cover consisted mainly of commercial blueberry, raspberry and cranberry crops which bloomed only for a short period of the bee colony cycle. This may result in a decline of local bee populations that otherwise require a season-long supply of forage to provision the colony. In the Lower Mainland of British Columbia, farmers rely heavily on honey bees to pollinate

blueberry crops, even though they are not as efficient as bumble bees in pollinating blueberry crops (Sampson and Cane 2000, Stubbs and Drummond 2001). Previous studies have suggested bumble bees reduce pollination deficit in berry crops and potentially increase the market value of berry crops (Ratti et al. 2008, Button and Elle 2014), however, with generally fewer nesting and foraging opportunities for bumble bees in farms, it is unlikely that wild bumble bee populations will reach levels necessary to reduce pollination deficit in berry crops, and at a scale that will benefit farmers substantially. Providing forage to temporally complement resource bloom from blueberry crops and nest sites can help to sustain bumble bees throughout the season and potentially increase their numbers.

The chances of nest founding increased at sites with more edge density. Margins between two land covers can offer additional forage and nesting sites to complement mass-flowering blueberry crops. Continuity of forage is important for nesting bumble bees who are without food when crop bloom ceases. This finding reiterates the importance of edge habitats for sustaining the population of wild pollinators adding to the growing literature (Lagerlöf et al. 1992, Bäckman and Tiainen 2002, Carvell et al. 2007). With little uncultivated land to spare for substantial management for wild bees and the heavy financial investments needed to compensate farmers who agree to take their land out of production for any conservation efforts, edge habitats which are usually uncultivated and require very little management for wild pollinator conservation might be a way to provide habitats to provide complementary forage and nesting resources for wild bumble bees in intensively managed agricultural landscapes.

The proportion of suburban cover decreased the chances of nest founding. Suburban development constitutes an important land use in the study region. The construction of settlements, paving, and roads may have resulted in a reduction in the quality and quantity of nesting sites and foraging resources for wild bumble bees. While suburban parks, home and community gardens were expected to provide floral resources for bees, considering the numerous studies that have suggested that suburban areas can support wild pollinators, floral resources in the suburban landscape in this study may have been of low quality. The combination of impervious non-habitat features, and low-quality floral resources may have rendered the suburban landscape in this study unattractive for nest searching bumble bee queens.

I demonstrate that bumble bees responded to the landscape at a large spatial scale at the nest founding stage, likely reflecting the selection of the most readily available habitat within the broader range of habitats in the landscape. However, the landscape did not explain colony success even when measured at any spatial scale likely reflecting a poor link between the measures of landscape structure used in this study as predictors of colony success. It is suggested that further studies should consider the inclusion of more detailed measurements of the landscape, such as the abundance and diversity of flowering plants, as more appropriate variables to explain colony success of wild bumble bees. I add to the literature, highlighting the importance of considering spatial scale in the analysis of bumble bee response to the landscape (Steffan-Dewenter et al. 2002, Goulson et al. 2010).

The results from this study have practical relevance for blueberry farmers who may wish to increase bumble bee abundances within their farms and potentially maximize pollination services to their crops. Blueberry farmers can encourage wild pollinators in their fields by maintaining and optimizing areas such as edge habitats (i.e., margins, verges) that are close to their fields to provide complementary forage and nest sites for populations of wild bees. Edge habitats seemed to attract bumble bee queens to nest and could serve as sources of pollinators who could forage in adjacent crop fields. This presents an opportunity for exchange, for example, a spill-over of pollinators from pollinator rich edge habitats to pollinator limited nearby crop fields. For growers, managing habitats for pollinators may be important for berry crops, for example, the Bluecrop cultivar which has a flower shape that results in fewer visits and encouraged nectar robbing by honey bees, therefore, reducing chances of pollen deposition (Courcelles et al. 2013). As such, Bluecrop may benefit more from bumble bee visitations. Maintaining edge habitats for pollinators can be unpopular among most blueberry farmers as many fear they draw bees away from their fields and reduce pollination services, however, (Morandin and Kremen 2013) have shown that in an agricultural landscape, managed hedgerows enhanced the population of wild bees and acted as net exporters of bees rather than concentrating pollinators, and that, the additional floral resources from hedgerows do not draw bees away from crop plants. This should alleviate the fears of many farmers.

FIGURES

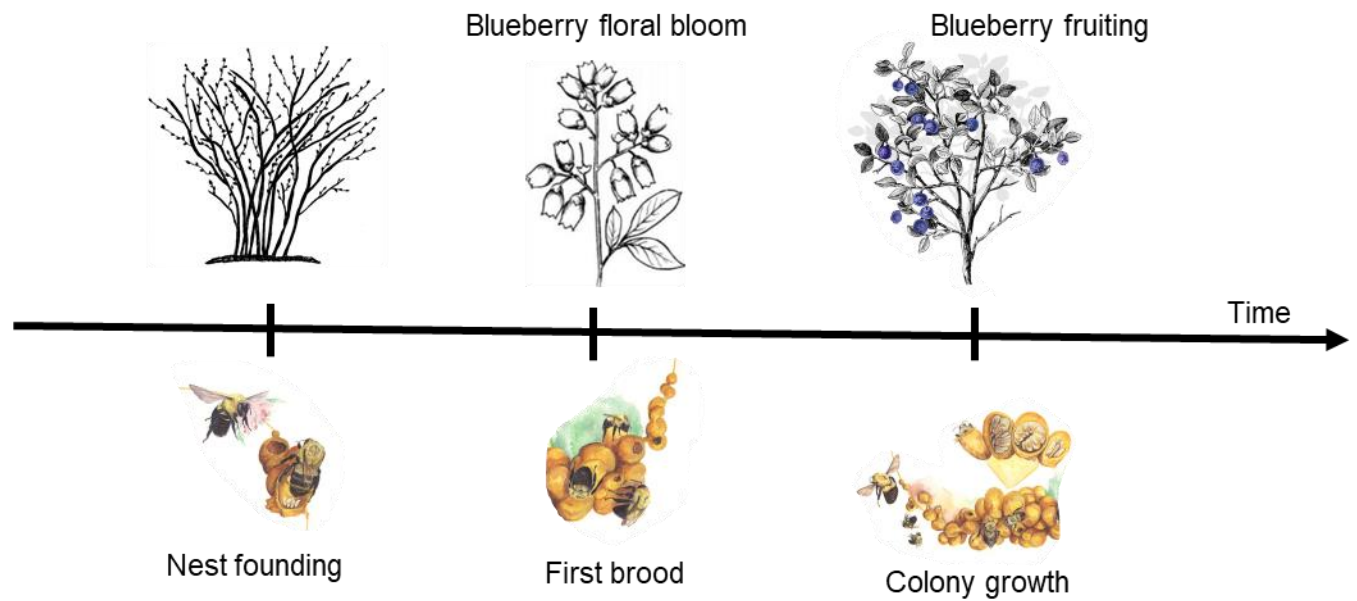


Figure 1: Bumble bee colony cycle and the availability of floral resources provided by blueberry crops. Blueberry crops provide copious floral resources after nest founding and early in the period of colony development (i.e., production of first brood), however, crop bloom ceases during the period of colony growth (i.e., production of more workers, increase in colony size) and up to the production of reproductives (i.e., new queens and males). Images from google images.

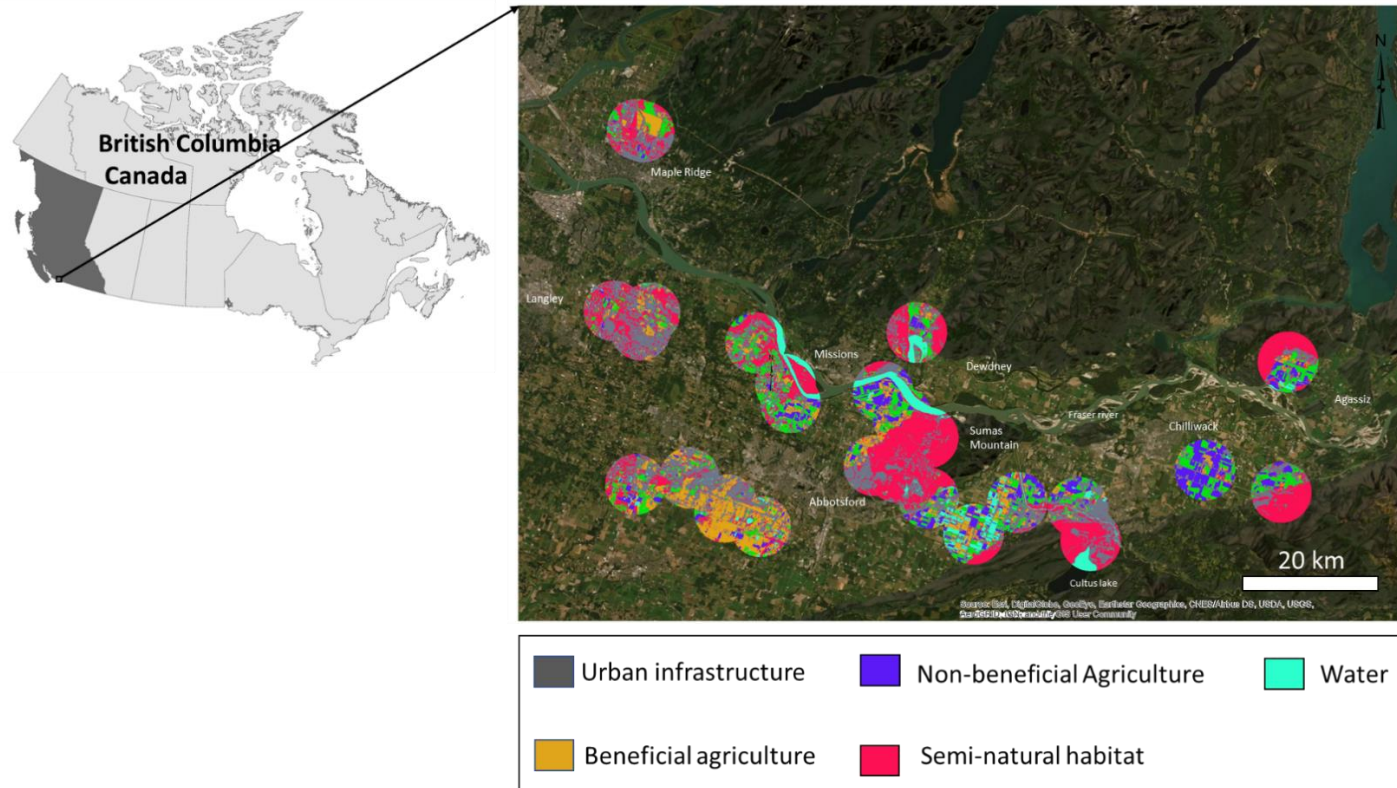


Figure 2: Location of study sites ($n= 27$) in the Lower Mainland, British Columbia, Canada. Land cover types were quantified using AAFC crop inventory satellite imagery (Annual Space-Based Crop Inventory for Canada 2019). From its original ~ 45 cover type classification, the raster imagery was reclassified by clustering classes into three groups: semi-natural cover (forest, shrubland, pasture, grassland, and wetlands), beneficial agricultural cover (blueberry, raspberry, and cranberry fields) and suburban cover (residential and built-up areas). The category on non-beneficial agriculture (maize, cereal, wheat, etc.) was excluded from the analysis, however, it is included in this figure for clarity on the range of land cover classes in the satellite imagery.

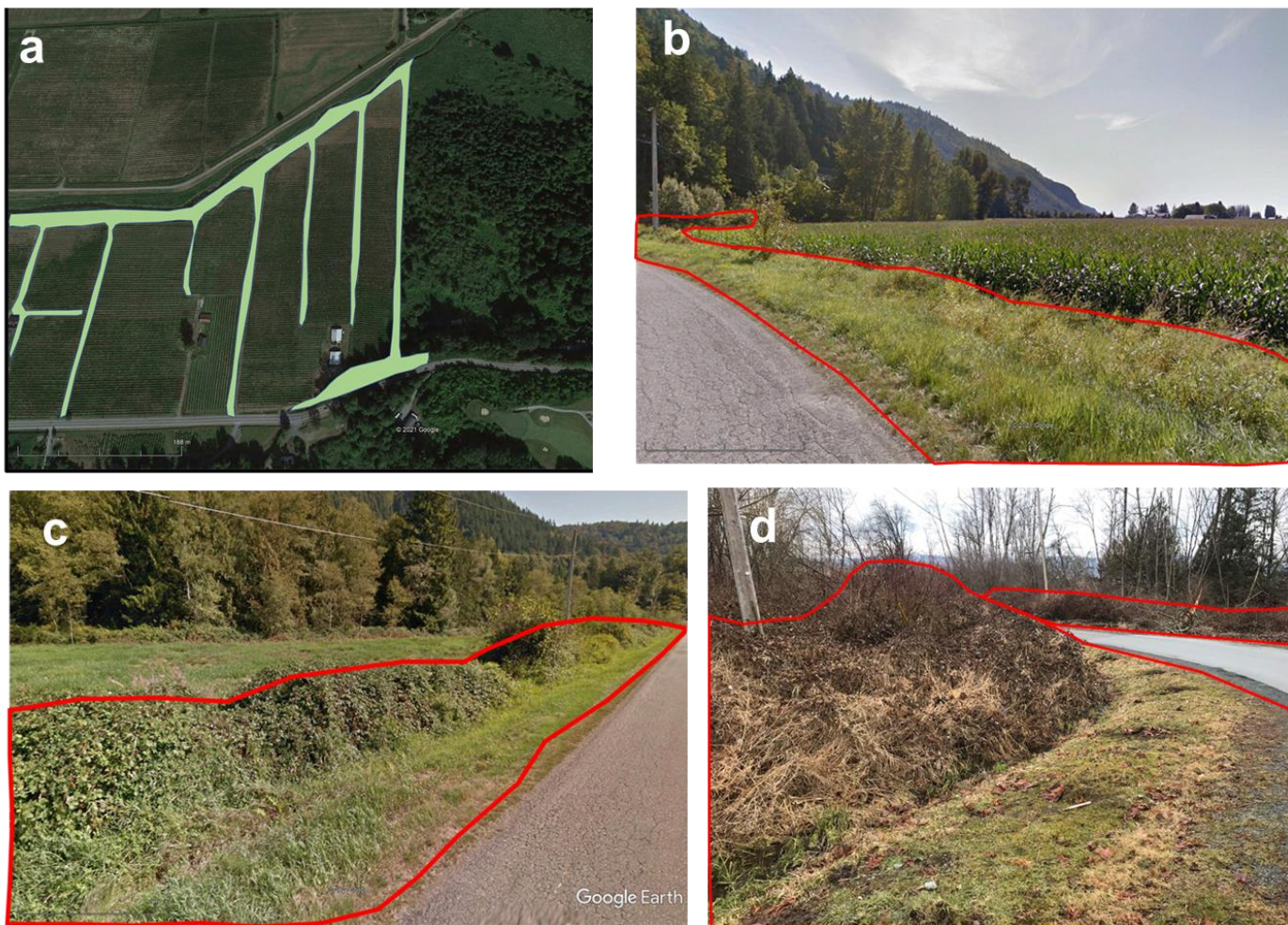


Figure 3: Visual (a) representation of edge habitats as shared margins (light green) between two land cover classes (b) edge habitat represented as grassy margins (location within red outline) (c) edge habitat represented as hedgerows with herbaceous vegetation (d) edge habitat represented as grassy margins with remnant herbaceous vegetation. Images from google earth imagery.

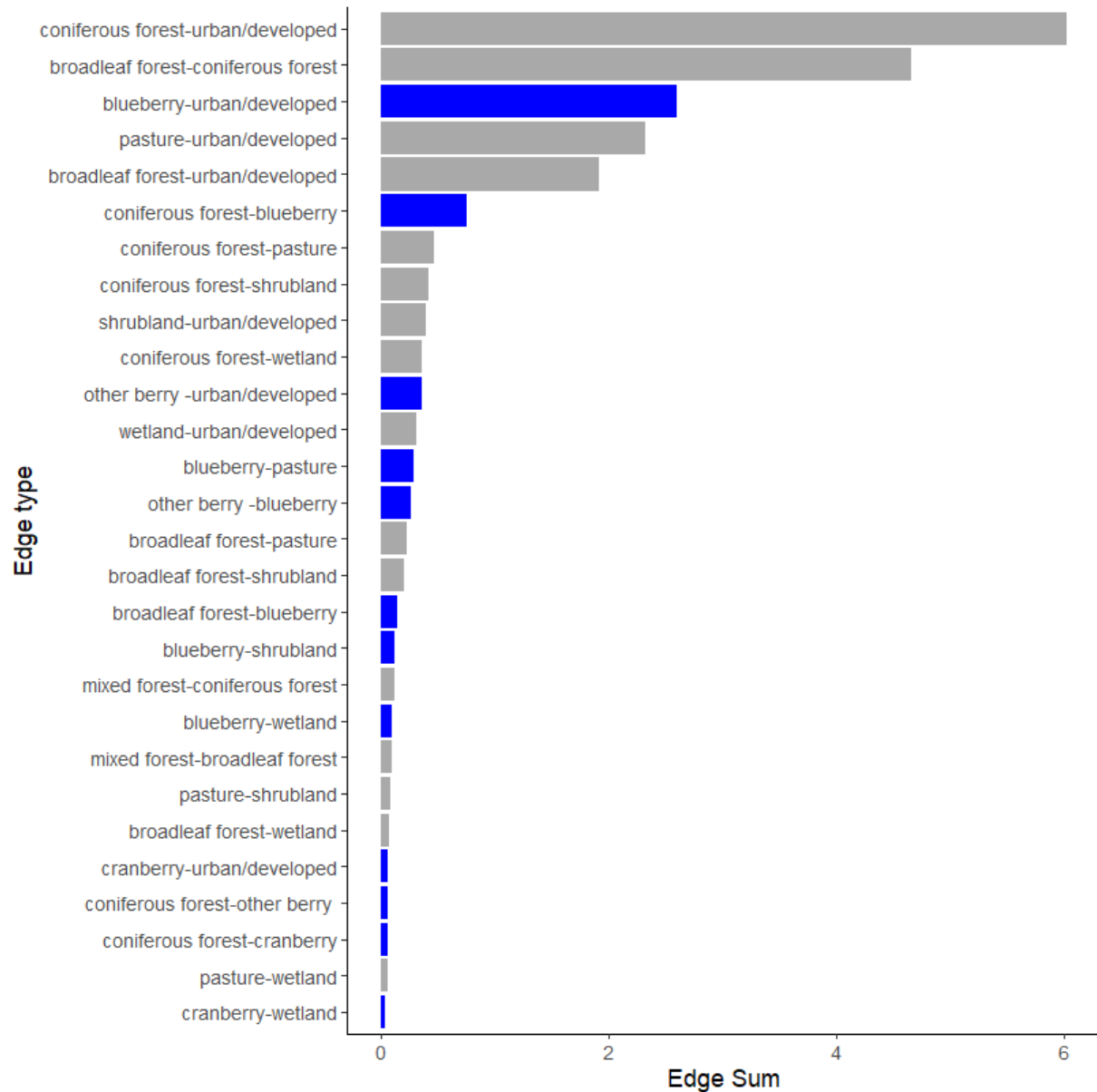


Figure 4: Edge amount (proportional sum) for each pair of land cover classes where edge represents the interface between habitat types. The sums are given for a combination of land cover classes for 27 study locations and quantified within a 2500 m radius of a bumble bee colony. Blue bars represent edges that are controlled by farmers.

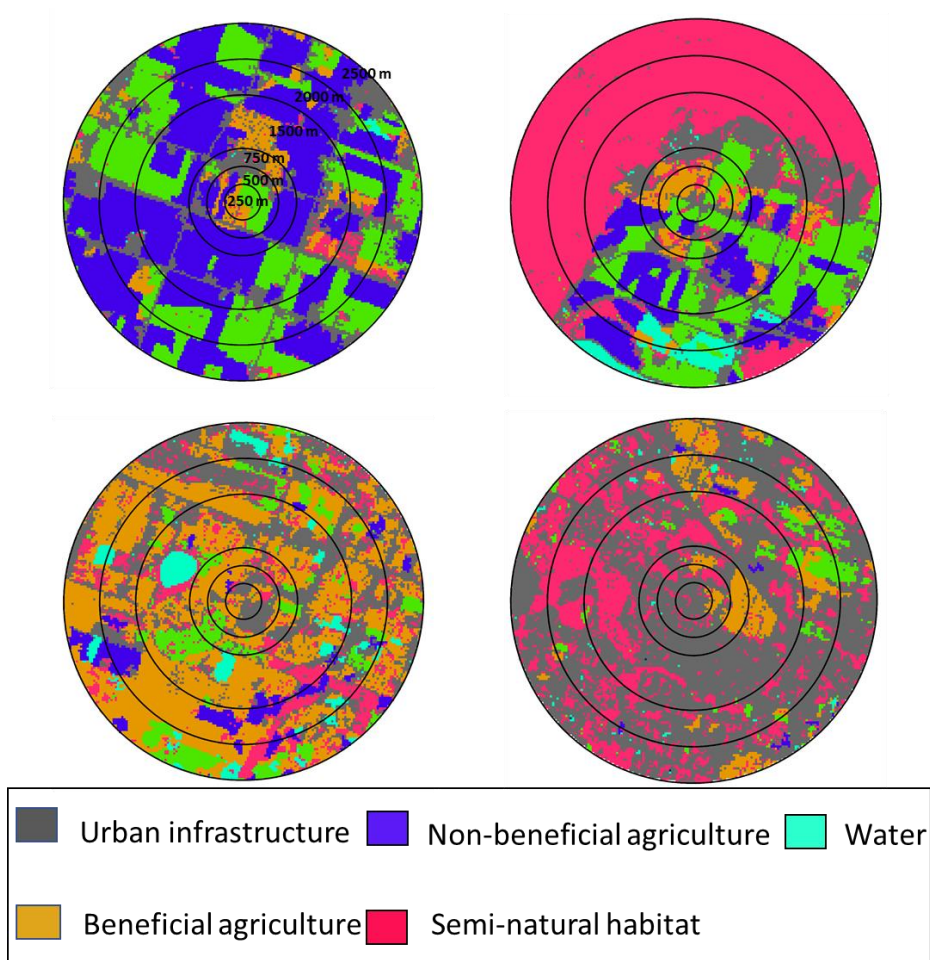


Figure 5: Four representative study sites with land cover types nested in six spatial scales (250 m, 500 m, 750 m, 1500, 2000 m, 2500 m) used in the analysis.



Figure 6: (a) An example of a location along ditch banks or uncultivated areas close to blueberry farms where underground boxes were placed, (b) Bumble bee nest lined with upholsterers' cotton to provide insulation and medium for nest establishment (c) Bumble bee box placed a few centimetres below the surface of the ground. (d) Bee box covered with excavated sod with a PVC tube leading to the nest and serving as entrance and exit route for bumble bee queen and workers.

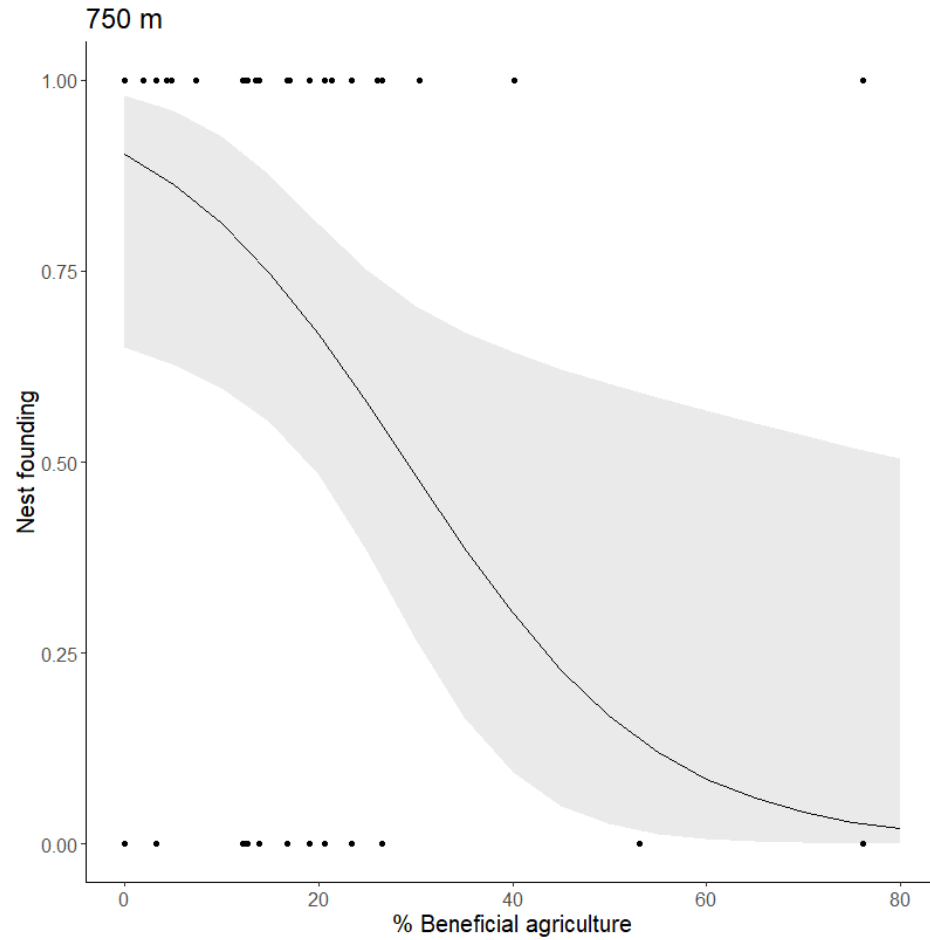


Figure 7: Partial regression plot of nest founding (black line) and the 95% confidence interval (grey region) describing the nest founding model at a 750 m spatial scale. This result supports the prediction that the proportion of beneficial agriculture in the landscape is negatively related to nest founding. Circles show data (N= 106).

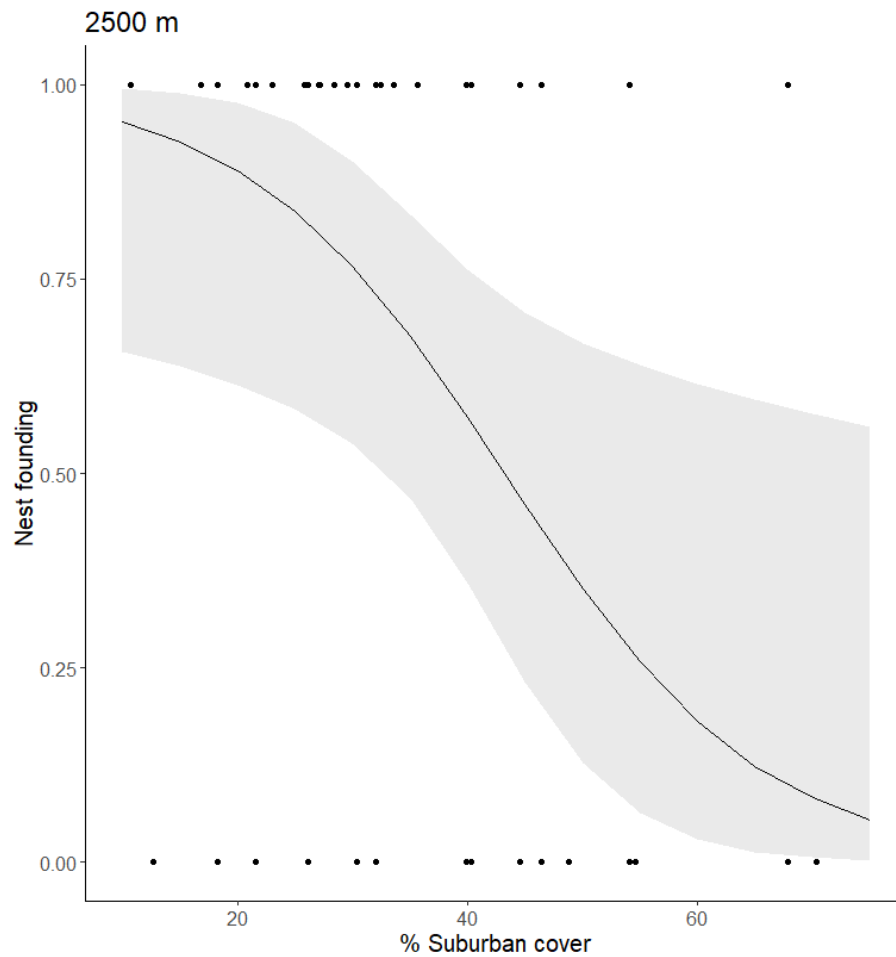


Figure 8: Partial regression plot of nest founding (black line) and 95 % confidence interval (grey region) describing the nest founding model at a 2500 m spatial scale. This result is against the prediction that the proportion of suburban cover in the landscape is positively related to nest founding. Circles show data (N=106).

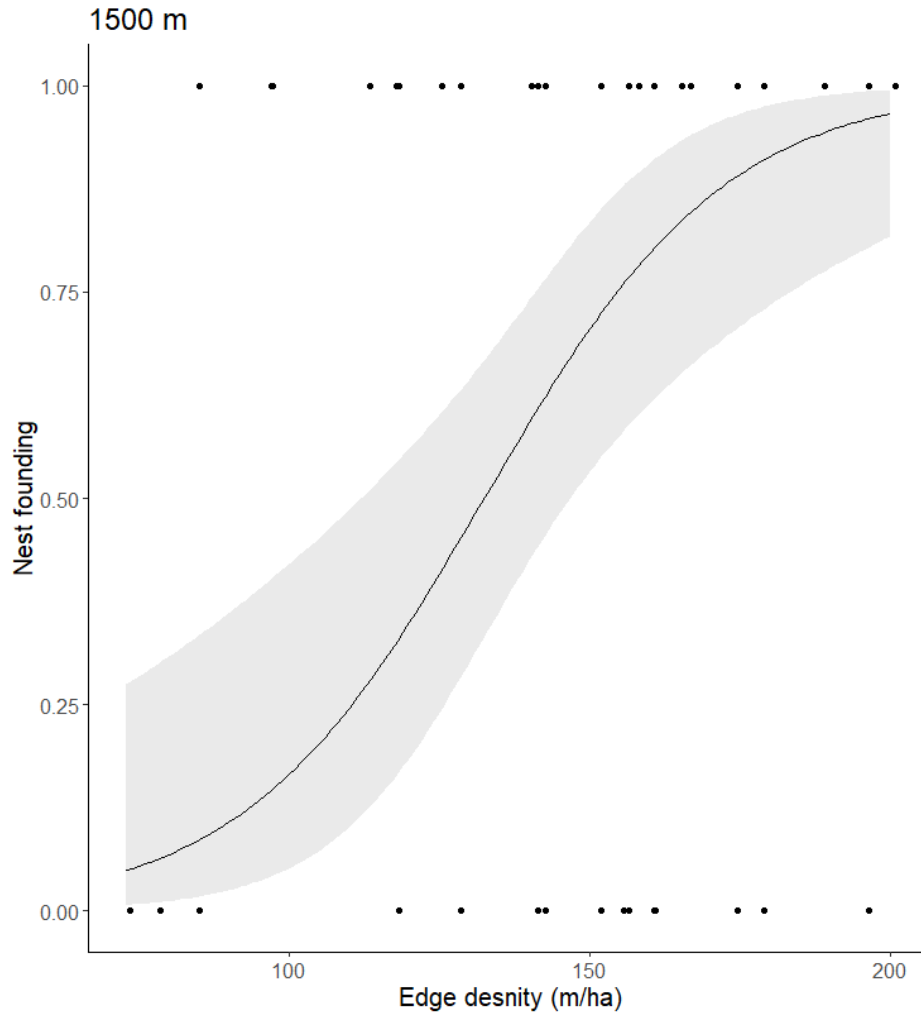


Figure 9: Partial regression plot of nest founding (black line) and the 95% confidence interval (grey region) describing the nest founding model at a 1500 m spatial scale. This result supports the prediction that edge density in the landscape is positively related to nest founding. Circles show data (N= 106).

TABLES

Table 1: Detailed land cover used in the regression analysis. Land use types were clustered into groups to form a single habitat category. Quantification was based on AAFC crop inventory data. Habitat categories were quantified within a 2500 m radius of bumble bee colony. The proportion of cover type, edge density per cover type, mean \pm SD (cover area), minimum and maximum cover area are given for 27 study locations.

Habitat category	Land-use	% Cover	Edge density (m/ha)	Mean area (ha) \pm SD	Minimum cover area	Maximum cover area
Semi-natural habitat	Wetland	1.23	7.80	0.35 \pm 3.12	0.09	81.45
	Coniferous forest	22.29	91.98	1.27 \pm 22.80	0.09	1346.67
	Pasture	10.90	28.32	6.6 \pm 15.87	0.09	206.19
	Mixed forest	0.14	1.44	0.17 \pm 0.38	0.09	6.48
	Broadleaf forest	7.73	50.59	0.63 \pm 5.77	0.09	274.59
	Grassland	0.01	0.08	0.09 \pm 0.02	0.09	0.18
	Shrubland	0.81	9.35	0.13 \pm 0.18	0.09	5.49
Suburban cover	Suburban/Developed	31.21	109.07	2.69 \pm 62.79	0.09	2561.40
Beneficial agriculture	Blueberry	8.46	29.43	4.99 \pm 24.47	0.09	605.25
	Cranberry	0.67	1.01	8.77 \pm 31.16	0.09	175.23
	Potato	0.57	1.39	4.85 \pm 4.94	0.09	22.23
	Other berry	1.20	3.89	3.63 \pm 6.28	0.09	45.18

Table 2: Mean and standard deviation (proportional) of edge for each pair of land cover classes where edge represents the interface between habitat types. The mean and standard deviation are given for a combination of land cover classes for 27 study locations and quantified within a 2500 m radius of bumble bee colony.

Land cover class	Mean	Standard deviation
grassland-urban/developed	0.0002	0.0004
grassland-shrubland	0.0000	0.0001
grassland-wetland	0.0000	0.0000
pasture-grassland	0.0000	0.0000
pasture-urban/developed	0.0858	0.0681
pasture-shrubland	0.0031	0.0026
pasture-wetland	0.0020	0.0030
blueberry-grassland	0.0000	0.0001
blueberry-pasture	0.0106	0.0082
blueberry-potato	0.0008	0.0017
blueberry-urban/developed	0.0962	0.0845
blueberry-shrubland	0.0043	0.0045
blueberry-wetland	0.0035	0.0044
cranberry-grassland	0.0000	0.0000
cranberry-pasture	0.0004	0.0007
cranberry-potato	0.0000	0.0002
cranberry-blueberry	0.0003	0.0006
cranberry-urban/developed	0.0022	0.0050
cranberry-shrubland	0.0004	0.0011
cranberry-wetland	0.0012	0.0040
other berry -grassland	0.0000	0.0000
other berry -pasture	0.0006	0.0009
other berry -potato	0.0001	0.0003
other berry -blueberry	0.0096	0.0246
other berry -cranberry	0.0000	0.0001
other berry -urban/developed	0.0132	0.0226
other berry -shrubland	0.0002	0.0004
other berry -wetland	0.0002	0.0003
coniferous forest-grassland	0.0001	0.0002
coniferous forest-pasture	0.0173	0.0167
coniferous forest-potato	0.0003	0.0007
coniferous forest-blueberry	0.0277	0.0279
coniferous forest-cranberry	0.0021	0.0054
coniferous forest-other berry	0.0022	0.0045
coniferous forest-urban/developed	0.2229	0.1215
coniferous forest-shrubland	0.0152	0.0148
coniferous forest-wetland	0.0133	0.0179

Table 2 continued

broadleaf forest-grassland	0.0000	0.0000
broadleaf forest-pasture	0.0082	0.0087
broadleaf forest-potato	0.0000	0.0001
broadleaf forest-blueberry	0.0052	0.0045
broadleaf forest-cranberry	0.0001	0.0002
broadleaf forest-other berry	0.0002	0.0003
broadleaf forest-coniferous forest	0.1725	0.1379
broadleaf forest-urban/developed	0.0709	0.0414
broadleaf forest-shrubland	0.0075	0.0048
broadleaf forest-wetland	0.0028	0.0022
mixed forest-grassland	0.0000	0.0000
mixed forest-pasture	0.0000	0.0001
mixed forest-potato	0.0000	0.0000
mixed forest-blueberry	0.0000	0.0001
mixed forest-cranberry	0.0000	0.0000
mixed forest-coniferous forest	0.0042	0.0077
mixed forest-broadleaf forest	0.0033	0.0053
mixed forest-urban/developed	0.0008	0.0015
mixed forest-shrubland	0.0000	0.0000
mixed forest-wetland	0.0000	0.0001
shrubland-urban/developed	0.0147	0.0067
wetland-urban/developed	0.0114	0.0097
wetland-shrubland	0.0009	0.0010

Table 3: Principal Component Analysis (PCA) showing eigenvector scores, Box-Cox exponents applied to transformations and constants added to measures of colony success before power transformation, and the proportion of variance in original data explained by the principal component axis. PCA was used to produce a single measure of colony success that summarized six measures of colony success.

Variable	PC1	PC2	Box-cox exponent	Constant
Wet weight	0.473	0.2287	ln	0.0005
Number of emerged cells	0.465	0.3301	ln	0.5
Number of Larvae	0.397	-0.397	-1	0.5
Number of Pupae	0.296	0.1626	-2	1
Number of Eggs	0.281	-0.796	-2	1
Number of honey and pollen pots	0.486	0.1472	-0.5	1
Proportion of variance	0.613	0.154		

Table 4: Nest founding model. Mixed model logistic regression predicting nest founding from the proportion of beneficial agriculture, edge density, the proportion of semi-natural habitat and the proportion of suburban cover. The table shows average parameter estimates and standard error (SE), z value and p-value for all parameters estimated in the models fitted at each spatial scale (250 m to 2500 m, 106 boxes and 27 sites). All continuous predictors are standardized. Marginal R^2 values are presented as measures of model fit and consider fixed effects only. Site identity was a random effect. Significant parameters are bolded. AIC_C and delta AIC_C scores for the full model at each scale in comparison with its null model.

Parameter	250 m				500 m				750 m			
	Estimate	SE	Z	P	Estimate	SE	Z	P	Estimate	SE	Z	P
% Beneficial agriculture	-0.36	1.27	-0.29	0.773	-1.85	1.17	-1.58	0.113	-1.60	0.70	-2.28	0.022
Edge density	1.02	0.51	1.99	0.047	1.08	0.53	2.02	0.043	1.38	0.43	3.22	0.001
% Semi-natural habitat	-0.04	1.38	-0.03	0.976	-1.04	1.13	-0.92	0.358	-0.63	0.59	-1.05	0.291
% Suburban cover	0.56	1.01	0.55	0.580	-0.94	0.78	-1.20	0.229	-0.73	0.49	-1.48	0.139
Marginal R²	0.232				0.240				0.364			
AIC_C	124.98				124.58				119.72			
ΔAIC_C	0.15				0.00				0.00			

Table 4 continued

Parameter	1500 m				2000 m				2500 m			
	Estimate	SE	Z	P	Estimate	SE	Z	P	Estimate	SE	Z	P
% Beneficial agriculture	-1.54	0.56	-2.74	0.006	-1.46	0.67	-2.17	0.030	-1.24	0.71	-1.77	0.077
Edge density	1.68	0.49	3.43	0.001	1.56	0.54	2.91	0.004	1.48	0.53	2.82	0.005
% Semi-natural habitat	0.02	0.47	0.044	0.965	0.03	0.58	0.05	0.959	-0.04	0.65	0.07	0.947
% Suburban cover	-0.77	0.42	-1.84	0.065	-1.21	0.56	-2.16	0.031	-1.34	0.60	-2.22	0.026
Marginal R²	0.426				0.357				0.353			
AIC_C	117.06				120.26				119.83			
ΔAIC_C	0.00				0.00				0.00			

Table 5: Colony success model. Generalised linear mixed model (gaussian distribution) predicting nest success from the proportion of beneficial agriculture, edge density, the proportion of semi-natural habitat, the proportion of suburban cover and the interaction between beneficial agriculture and edge density. The table shows average parameter estimates and standard error (SE), denominator degrees of freedom, t value and p-value for all parameters estimated in the models fitted at each spatial scale (250 m to 2500 m, 63 boxes, 23 sites). All continuous predictors are standardized. Marginal R^2 values are presented as measures of model fit and consider fixed effects only. Site identity was a random effect. Significant parameters are bolded. AIC_C and delta AIC_C scores for the full model at each scale in comparison with its null model.

	250 m					500 m					750 m				
Parameter	Estimate	SE	DF	t	P	Estimate	SE	DF	t	P	Estimate	SE	DF	t	P
% Beneficial agriculture (BA)	0.23	0.60	35.81	0.38	0.708	0.63	0.44	16.55	1.44	0.167	0.43	0.32	21.05	1.35	0.192
Edge density (ED)	-0.64	0.27	30.23	- 2.34	0.026	-0.10	0.31	26.69	-0.32	0.755	0.09	0.30	19.38	0.30	0.764
% Semi-natural habitat	0.11	0.70	33.43	0.16	0.873	0.30	0.49	16.02	0.61	0.553	0.46	0.34	16.60	1.36	0.193
% Suburban cover	0.50	0.65	35.11	0.78	0.442	0.88	0.43	13.91	2.04	0.061	0.68	0.33	14.52	2.05	0.059
Interaction (BA*ED)	0.39	0.20	36.28	1.91	0.064	0.45	0.25	27.79	1.84	0.077	0.55	0.28	26.48	1.96	0.061
Marginal R²	0.163					0.137					0.123				
AIC_C	271.29					273.19					274.81				
ΔAIC_C	4.51					6.41					8.04				

Table 5 continued

	1500 m					2000 m					2500 m				
Parameter	Estimate	SE	DF	t	P	Estimate	SE	DF	t	P	Estimate	SE	DF	t	P
% Beneficial agriculture (BA)	-0.32	0.40	37.69	-0.79	0.433	-0.85	0.53	39.69	-1.61	0.115	-0.32	0.48	33.75	-	0.516
Edge density (ED)	0.44	0.36	22.39	1.22	0.234	0.77	0.43	25.71	1.77	0.088	0.25	0.36	21.76	0.66 0.69	0.499
% Semi-natural habitat	0.15	0.35	21.10	0.44	0.667	-0.01	0.38	21.84	-0.04	0.971	0.14	0.40	22.89	0.34	0.734
% Suburban cover	0.11	0.34	15.25	0.32	0.756	-0.01	0.35	17.15	-0.02	0.987	0.02	0.40	18.56	0.06	0.951
Interaction (BA*ED)	0.66	0.35	26.68	1.89	0.069	1.16	0.48	31.78	2.42	0.022	0.72	0.35	25.74	2.06	0.050
Marginal R²	0.084					0.107					0.085				
AIC_C	276.58					274.15					276.29				
ΔAIC_C	9.80					7.30					9.51				

Table 6: Model comparison using AIC_C and model weight for the models on nest founding in relation to landscape fitted at each spatial scale (250 m to 2500 m). Models are presented in order with the first model being the best among the list of the models compared according to its lowest delta AIC_C and highest AIC_C weight value. Delta AIC_C represents the differences in the AIC_C score relative to the minimum AIC_C, K represents the number of parameters in the model, AIC_C weight is the proportion of the total amount of predictive power of the set of models being compared, cumulative weight is the sum of delta AIC_C weight, log-likelihood describes how plausible the model is, given the data.

Model	Scale (m)	K	AICc	Delta AICc	AICc weight	Cumulative weight	Log-likelihood
md.1500	1500	6	117.06	0	0.56	0.56	-52.11
md.750	750	6	119.72	2.65	0.15	0.71	-53.43
md.2500	2500	6	119.83	2.77	0.14	0.85	-53.49
md.2000	2000	6	120.26	3.19	0.11	0.96	-53.7
md.500	500	6	124.58	7.52	0.01	0.98	-55.87
md.null	-	2	124.82	7.76	0.01	0.99	-60.35
md.250	250	6	124.98	7.91	0.01	1	-56.06

Table 7: Model comparison using AIC_C and model weight for the models on colony success in relation to landscape fitted at each spatial scale (250 m to 2500 m). Models are presented in order with the first model being the best among the list of the models compared according to its lowest delta AIC_C and highest AIC_C weight value. Delta AIC_C represents the differences in the AIC_C score relative to the minimum AIC_C, K represents the number of parameters in the model, AIC_C weight is the proportion of the total amount of predictive power of the set of models being compared, cumulative weight is the sum of delta AIC_C weight, log-likelihood describes how plausible the model is, given the data.

Model	Scale (m)	K	AICc	Delta AICc	AICc weight	Cumulative weight	Log-likelihood
mod.null	-	3	266.78	0	0.83	0.83	-130.19
mod.250	250	8	271.29	4.51	0.09	0.92	-126.31
mod.500	500	8	273.19	6.41	0.03	0.95	-127.26
mod.2000	2000	8	274.15	7.37	0.02	0.97	-127.74
mod.750	750	8	274.81	8.04	0.01	0.99	-128.07
mod.2500	2500	8	276.29	9.51	0.01	0.99	-128.81
mod.1500	1500	8	276.58	9.8	0.01	1	-128.96

LITERATURE CITED

- Adhikari, S., L. A. Burkle, K. M. O'Neill, D. K. Weaver, and F. D. Menalled. 2019. Dryland organic farming increases floral resources and bee colony success in highly simplified agricultural landscapes. *Agriculture, Ecosystems & Environment* **270**:9-18.
- Alford, D. 1970. The incipient stages of development of bumblebee colonies. *Insectes Sociaux* **17**:1-10.
- Anderson, D., and K. Burnham. 2004. Model selection and multi-model inference. Second. NY: Springer-Verlag **63**:10.
- Annual Space-Based Crop Inventory for Canada. 2019. Centre for Agroclimate, Geomatics and Earth Observation, Science and Technology Branch, Agriculture and Agri-Food Canada.
- Auestad, I., A. Norderhaug, and I. Austad. 1999. Road verges-species-rich habitats. *Aspects of Applied Biology* **54**:269-274.
- Bäckman, J.-P. C., and J. Tiainen. 2002. Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera: Bombus and Psithyrus). *Agriculture, Ecosystems & Environment* **89**:53-68.
- Baldock, K. C., M. A. Goddard, D. M. Hicks, W. E. Kunin, N. Mitschunas, H. Morse, L. M. Osgathorpe, S. G. Potts, K. M. Robertson, and A. V. Scott. 2019. A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nature ecology & evolution* **3**:363-373.
- Banaszak-Cibicka, W., and M. Żmihorski. 2012. Wild bees along an urban gradient: winners and losers. *Journal of Insect Conservation* **16**:331-343.
- Bartual, A. M., L. Sutter, G. Bocci, A.-C. Moonen, J. Cresswell, M. Entling, B. Giffard, K. Jacot, P. Jeanneret, and J. Holland. 2019. The potential of different semi-natural habitats to sustain pollinators and natural enemies in European agricultural landscapes. *Agriculture, Ecosystems & Environment* **279**:43-52.
- Bennett, A. B., and R. Isaacs. 2014. Landscape composition influences pollinators and pollination services in perennial biofuel plantings. *Agriculture, Ecosystems & Environment* **193**:1-8.
- Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* **65**:23-35.
- Button, L., and E. Elle. 2014. Wild bumble bees reduce pollination deficits in a crop mostly visited by managed honey bees. *Agriculture, Ecosystems & Environment* **197**:255-263.
- Campbell, B., H. Khachatryan, and A. Rihn. 2017. Pollinator-friendly plants: reasons for and barriers to purchase. *HortTechnology* **27**:831-839.
- Cane, J. H., R. L. Minckley, L. J. Kervin, T. a. H. Roulston, and N. M. Williams. 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecological Applications* **16**:632-644.
- Cardinal, S., S. L. Buchmann, and A. L. Russell. 2018. The evolution of floral sonication, a pollen foraging behavior used by bees (Anthophila). *Evolution* **72**:590-600.
- Carvell, C., W. R. Meek, R. F. Pywell, D. Goulson, and M. Nowakowski. 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology* **44**:29-40.
- Carvell, C., J. Osborne, A. Bourke, S. Freeman, R. Pywell, and M. Heard. 2011. Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality. *Ecological Applications* **21**:1760-1771.
- Cavigliasso, P., C. C. Phifer, E. M. Adams, D. Flaspohler, G. P. Gennari, J. A. Licata, and N. P. Chacoff. 2020. Spatio-temporal dynamics of landscape use by the bumblebee *Bombus pauloensis* (Hymenoptera: Apidae) and its relationship with pollen provisioning. *PLoS One* **15**:e0216190.
- Clausen, M. 2017. Evaluating field margins for wild bee conservation at the farm and landscape- scale in the agricultural land reserve of Delta, British Columbia. University of British Columbia.

- Courcelles, D., L. Button, and E. Elle. 2013. Bee visit rates vary with floral morphology among highbush blueberry cultivars (*Vaccinium corymbosum* L.). *Journal of Applied Entomology* **137**:693-701.
- Crone, E. E., and N. M. Williams. 2016. Bumble bee colony dynamics: quantifying the importance of land use and floral resources for colony growth and queen production. *Ecology Letters* **19**:460-468.
- Del Barrio, J. G., M. Ortega, A. V. De La Cueva, and R. Elena-Rosselló. 2006. The influence of linear elements on plant species diversity of Mediterranean rural landscapes: Assessment of different indices and statistical approaches. *Environmental monitoring and assessment* **119**:137-159.
- Dempster, J., and E. Pollard. 1981. Fluctuations in resource availability and insect populations. *Oecologia* **50**:412-416.
- Diaz-Forero, I., V. Kuusemets, M. Mänd, A. Liivamägi, T. Kaart, and J. Luig. 2013. Influence of local and landscape factors on bumblebees in semi-natural meadows: a multiple-scale study in a forested landscape. *Journal of Insect Conservation* **17**:113-125.
- Diekötter, T., F. Peter, B. Jauker, V. Wolters, and F. Jauker. 2014. Mass-flowering crops increase richness of cavity-nesting bees and wasps in modern agro-ecosystems. *Gcb Bioenergy* **6**:219-226.
- Diekötter, T., K. Walther-Hellwig, M. Conradi, M. Suter, and R. Frankl. 2006. Effects of landscape elements on the distribution of the rare bumblebee species *Bombus muscorum* in an agricultural landscape. *Biodiversity & Conservation* **15**:57-68.
- Doligez, B., T. Boulinier, and D. Fath. 2008. Habitat selection and habitat suitability preferences. *Encyclopedia of Ecology*:1810-1830.
- Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. *Oikos*:169-175.
- E-Flora BC: Electronic Atlas of the Flora of British Columbia. 2021. URL: <https://ibis.geog.ubc.ca/biodiversity/eflora/efloraacknowledgements.html> (accessed 26/1/2021).
- ESRI, R. 2011. ArcGIS desktop: release 10. Environmental Systems Research Institute, CA.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*:487-515.
- Fahrig, L., J. Baudry, L. Brotons, F. G. Burel, T. O. Crist, R. J. Fuller, C. Sirami, G. M. Siriwardena, and J. L. Martin. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters* **14**:101-112.
- Fahrig, L., J. Girard, D. Duro, J. Pasher, A. Smith, S. Javorek, D. King, K. F. Lindsay, S. Mitchell, and L. Tischendorf. 2015. Farmlands with smaller crop fields have higher within-field biodiversity. *Agriculture, Ecosystems & Environment* **200**:219-234.
- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* **8**:50-59.
- Fetridge, E. D., J. S. Ascher, and G. A. Langellotto. 2008. The bee fauna of residential gardens in a suburb of New York City (Hymenoptera: Apoidea). *Annals of the Entomological Society of America* **101**:1067-1077.
- Finstad, A. G., S. Einum, O. Ugedal, and T. Forseth. 2009. Spatial distribution of limited resources and local density regulation in juvenile Atlantic salmon. *Journal of Animal Ecology*:226-235.
- Fox, J., and G. Monette. 1992. Generalized collinearity diagnostics. *Journal of the American Statistical Association* **87**:178-183.
- Fróna, D., J. Szenderák, and M. Harangi-Rákos. 2019. The Challenge of Feeding the World. *Sustainability* **11**:5816.
- Gaillard, J.-M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat–performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**:2255-2265.
- Gallai, N., J.-M. Salles, J. Settele, and B. E. Vaissière. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics* **68**:810-821.
- Garbuzov, M., and F. L. Ratnieks. 2014. Quantifying variation among garden plants in attractiveness to bees and other flower-visiting insects. *Functional Ecology* **28**:364-374.

- Gervais, A., V. Fournier, and M. Bélisle. 2020. Agricultural landscape composition affects the development and life expectancy of colonies of *Bombus impatiens*. *Ecosphere* **11**:e03142.
- Geslin, B., V. Le Féon, M. Folschweiller, F. Flacher, D. Carmignac, E. Motard, S. Perret, and I. Dajoz. 2016. The proportion of impervious surfaces at the landscape scale structures wild bee assemblages in a densely populated region. *Ecology and evolution* **6**:6599-6615.
- Goulson, D. 2010. *Bumblebees: behaviour, ecology, and conservation*. Oxford University Press, New York.
- Goulson, D., W. Hughes, L. Derwent, and J. Stout. 2002. Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. *Oecologia* **130**:267-273.
- Goulson, D., O. Lepais, S. O'connor, J. L. Osborne, R. A. Sanderson, J. Cussans, L. Goffe, and B. Darvill. 2010. Effects of land use at a landscape scale on bumblebee nest density and survival. *Journal of Applied Ecology* **47**:1207-1215.
- Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. *Oecologia* **153**:589-596.
- Hagen, M., M. Wikelski, and W. D. Kissling. 2011. Space use of bumblebees (*Bombus* spp.) revealed by radio-tracking. *PLoS One* **6**:e19997.
- Hald, A. 2002. Impact of agricultural fields on vegetation of stream border ecotones in Denmark. *Agriculture, Ecosystems & Environment* **89**:127-135.
- Heinrich, B. 1979. *Bumblebee economics*. Harvard University Press, United States of America.
- Herzon, I., and J. Helenius. 2008. Agricultural drainage ditches, their biological importance and functioning. *Biological Conservation* **141**:1171-1183.
- Hesselbarth, M. H., M. Sciaini, K. A. With, K. Wiegand, and J. Nowosad. 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography* **42**:1648-1657.
- Hines, H. M., and S. D. Hendrix. 2005. Bumble bee (Hymenoptera: Apidae) diversity and abundance in tallgrass prairie patches: effects of local and landscape floral resources. *Environmental Entomology* **34**:1477-1484.
- Hobbs, G., J. Virotek, and W. Nummi. 1960. Establishment of *Bombus* spp. (Hymenoptera: Apidae) in artificial domiciles in southern Alberta. *The Canadian Entomologist* **92**:868-872.
- Holland, J. D., D. G. Bert, and L. Fahrig. 2004. Determining the spatial scale of species' response to habitat. *BioScience* **54**:227-233.
- Holland, J. D., L. Fahrig, and N. Cappuccino. 2005. Body size affects the spatial scale of habitat-beetle interactions. *Oikos* **110**:101-108.
- Holland, J. M., J. C. Douma, L. Crowley, L. James, L. Kor, D. R. Stevenson, and B. M. Smith. 2017. Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. *Agronomy for Sustainable Development* **37**:31.
- Holzschuh, A., C. F. Dormann, T. Tschardtke, and I. Steffan-Dewenter. 2013. Mass-flowering crops enhance wild bee abundance. *Oecologia* **172**:477-484.
- Holzschuh, A., I. Steffan-Dewenter, and T. Tschardtke. 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *Journal of Animal Ecology* **79**:491-500.
- Isaacs, R., and A. K. Kirk. 2010. Pollination services provided to small and large highbush blueberry fields by wild and managed bees. *Journal of Applied Ecology* **47**:841-849.
- Javorek, S., K. Mackenzie, and S. Vander Kloet. 2002. Comparative pollination effectiveness among bees (Hymenoptera: Apoidea) on lowbush blueberry (Ericaceae: *Vaccinium angustifolium*). *Annals of the Entomological Society of America* **95**:345-351.
- Jha, S., and C. Kremen. 2013a. Resource diversity and landscape-level homogeneity drive native bee foraging. *Proceedings of the National Academy of Sciences* **110**:555-558.
- Jha, S., and C. Kremen. 2013b. Urban land use limits regional bumble bee gene flow. *Molecular ecology* **22**:2483-2495.

- Jonsen, I. D., and L. Fahrig. 1997. Response of generalist and specialist insect herbivores to landscape spatial structure. *Landscape Ecology* **12**:185-197.
- Kells, A. R., and D. Goulson. 2003. Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK. *Biological Conservation* **109**:165-174.
- Kerr, J. T., and I. Deguise. 2004. Habitat loss and the limits to endangered species recovery. *Ecology Letters* **7**:1163-1169.
- Klein, A.-M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences* **274**:303-313.
- Koch, J., J. Strange, and P. Williams. 2012. Guide to Bumble Bees of the Western United States. USDA Forest Service/Pollinator Partnership, San Fransisco, California.
- Kremen, C., M. Albrecht, and L. Ponisio. 2019. Restoring pollinator communities and pollination services in hedgerows in intensively managed agricultural landscapes. Pages 163-185.
- Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences* **99**:16812-16816.
- Lagerlöf, J., J. Stark, and B. Svensson. 1992. Margins of agricultural fields as habitats for pollinating insects. *Agriculture, Ecosystems & Environment* **40**:117-124.
- Landis, D. A. 2017. Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic and Applied Ecology* **18**:1-12.
- Lanterman, J., and K. Goodell. 2018. Bumble bee colony growth and reproduction on reclaimed surface coal mines. *Restoration Ecology* **26**:183-194.
- Lanterman, J., P. Reeher, R. J. Mitchell, and K. Goodell. 2019. Habitat preference and phenology of nest seeking and foraging spring bumble bee queens in northeastern North America (Hymenoptera: Apidae: *Bombus*). *The American Midland Naturalist* **182**:131-159.
- Lepais, O., B. Darvill, S. O'connor, J. L. Osborne, R. A. Sanderson, J. Cussans, L. Goffe, and D. Goulson. 2010. Estimation of bumblebee queen dispersal distances using sibship reconstruction method. *Molecular ecology* **19**:819-831.
- Lin, Y.-T. K., and G. O. Batzli. 2001. The influence of habitat quality on dispersal, demography, and population dynamics of voles. *Ecological Monographs* **71**:245-275.
- Ma, M., R. Hietala, M. Kuussaari, and J. Helenius. 2013. Impacts of edge density of field patches on plant species richness and community turnover among margin habitats in agricultural landscapes. *Ecological Indicators* **31**:25-34.
- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *The American Naturalist* **100**:603-609.
- MacKenzie, K. E. 1997. Pollination requirements of three highbush blueberry (*Vaccinium corymbosum* L.) cultivars. *Journal of the American Society for Horticultural Science* **122**:891-896.
- MacKenzie, K. E., and M. L. Winston. 1984. Diversity and abundance of native bee pollinators on berry crops and natural vegetation in the lower Fraser Valley, British Columbia. *The Canadian Entomologist* **116**:965-974.
- Makinson, J., J. L. Woodgate, A. Reynolds, E. A. Capaldi, C. J. Perry, and L. Chittka. 2019. Harmonic radar tracking reveals random dispersal pattern of bumblebee (*Bombus terrestris*) queens after hibernation. *Scientific Reports* **9**.
- Marshall, E. 2004. Agricultural landscapes: field margin habitats and their interaction with crop production. *Journal of Crop Improvement* **12**:365-404.
- Marshall, E., and A. Moonen. 2002. Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems & Environment* **89**:5-21.
- Martin, A. E., and L. Fahrig. 2012. Measuring and selecting scales of effect for landscape predictors in species-habitat models. *Ecological Applications* **22**:2277-2292.
- Martin, E. A., M. Dainese, Y. Clough, A. Báldi, R. Bommarco, V. Gagic, M. P. Garratt, A. Holzschuh, D. Kleijn, and A. Kovács-Hostyánszki. 2019. The interplay of landscape composition and

- configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters* **22**:1083-1094.
- Matson, P. A., W. J. Parton, A. G. Power, and M. J. Swift. 1997. Agricultural intensification and ecosystem properties. *Science* **277**:504-509.
- Matteson, K. C., J. S. Ascher, and G. A. Langellotto. 2008. Bee richness and abundance in New York City urban gardens. *Annals of the Entomological Society of America* **101**:140-150.
- McGarigal, K., and B. J. Marks. 1995. McGarigal, K., Marks, B.J., 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. **351**.
- McGregor, S. E. 1976. Insect pollination of cultivated crop plants. Agricultural Research Service, US Department of Agriculture.
- McIntyre, N. E. 2000. Ecology of urban arthropods: a review and a call to action. *Annals of the Entomological Society of America* **93**:825-835.
- Morandin, L. A., and C. Kremen. 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecological Applications* **23**:829-839.
- Nicholls, C. I., and M. A. Altieri. 2013. Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. *Agronomy for Sustainable Development* **33**:257-274.
- Noordijk, J., I. Raemakers, A. Schaffers, and K. Sýkora. 2009. Arthropod richness in roadside verges in the Netherlands. *Terrestrial Arthropod Reviews* **2**:63-76.
- Öckinger, E., and H. G. Smith. 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology* **44**:50-59.
- Osborne, J., S. Clark, R. Morris, I. Williams, J. Riley, A. Smith, D. Reynolds, and A. Edwards. 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology* **36**:519-533.
- Osborne, J. L., A. P. Martin, N. L. Carreck, J. L. Swain, M. E. Knight, D. Goulson, R. J. Hale, and R. A. Sanderson. 2008a. Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology* **77**:406-415.
- Osborne, J. L., A. P. Martin, C. R. Shortall, A. D. Todd, D. Goulson, M. E. Knight, R. J. Hale, and R. A. Sanderson. 2008b. Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *Journal of Applied Ecology* **45**:784-792.
- Osborne, J. L., I. H. Williams, and S. A. Corbet. 1991. Bees, pollination and habitat change in the European community. *Bee world* **72**:99-116.
- Persson, A. S., and H. G. Smith. 2013. Seasonal persistence of bumblebee populations is affected by landscape context. *Agriculture, Ecosystems & Environment* **165**:201-209.
- Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* **25**:345-353.
- Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology* **84**:2628-2642.
- Proesmans, W., G. Smagghe, I. Meeus, D. Bonte, and K. Verheyen. 2019. The effect of mass-flowering orchards and semi-natural habitat on bumblebee colony performance. *Landscape Ecology* **34**:1033-1044.
- Pyke, G. H. 1984. Optimal foraging theory: a critical review. *Annual review of ecology and systematics* **15**:523-575.
- R Core Team. 2019. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2015. R Foundation for Statistical Computing.
- Rao, S., G. D. Hoffman, J. Kirby, and D. Horne. 2019. Remarkable long-distance returns to a forage patch by artificially displaced wild bumble bees (Hymenoptera: Apidae). *Journal of Apicultural Research* **58**:522 - 530.
- Ratti, C. M., H. A. Higo, T. L. Griswold, and M. L. Winston. 2008. Bumble bees influence berry size in commercial *Vaccinium* spp. cultivation in British Columbia. *The Canadian Entomologist* **140**:348-363.

- Redhead, J. W., S. Dreier, A. F. Bourke, M. S. Heard, W. C. Jordan, S. Sumner, J. Wang, and C. Carvell. 2016. Effects of habitat composition and landscape structure on worker foraging distances of five bumble bee species. *Ecological Applications* **26**:726-739.
- Robinson, R. A., and W. J. Sutherland. 2002. Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology* **39**:157-176.
- Roulston, T. a. H., and K. Goodell. 2011. The role of resources and risks in regulating wild bee populations. *Annual review of entomology* **56**:293-312.
- Rundlöf, M., A. S. Persson, H. G. Smith, and R. Bommarco. 2014. Late-season mass-flowering red clover increases bumble bee queen and male densities. *Biological Conservation* **172**:138-145.
- Sampson, B. J., and J. H. Cane. 2000. Pollination efficiencies of three bee (Hymenoptera: Apoidea) species visiting rabbiteye blueberry. *Journal of Economic Entomology* **93**:1726-1731.
- Samuelson, A. E., R. J. Gill, M. J. Brown, and E. Leadbeater. 2018. Lower bumblebee colony reproductive success in agricultural compared with urban environments. *Proceedings of the Royal Society B: Biological Sciences* **285**:20180807.
- Smith, H., R. Feber, P. Johnson, K. McCallum, S. P. Jensen, M. Younes, and D. Macdonald. 1993. The conservation management of arable field margins. *English Nature Peterborough*.
- Spiesman, B. J., A. Bennett, R. Isaacs, and C. Gratton. 2017. Bumble bee colony growth and reproduction depend on local flower dominance and natural habitat area in the surrounding landscape. *Biological Conservation* **206**:217-223.
- Stanley, D. A., and J. C. Stout. 2013. Quantifying the impacts of bioenergy crops on pollinating insect abundance and diversity: a field-scale evaluation reveals taxon-specific responses. *Journal of Applied Ecology* **50**:335-344.
- Steffan-Dewenter, I., U. Münzenberg, C. Bürger, C. Thies, and T. Tscharnkte. 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* **83**:1421-1432.
- Steffan-Dewenter, I. 2003. Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology* **17**:1036-1044.
- Stubbs, C. S., and F. A. Drummond. 2001. *Bombus impatiens* (Hymenoptera: Apidae): an alternative to *Apis mellifera* (Hymenoptera: Apidae) for lowbush blueberry pollination. *Journal of Economic Entomology* **94**:609-616.
- Suzuki, Y., L. G. Kawaguchi, D. T. Munidasa, and Y. Toquenaga. 2009. Do bumble bee queens choose nest sites to maximize foraging rate? Testing models of nest site selection. *Behavioral Ecology and Sociobiology* **63**:1353-1362.
- Svensson, B., J. Lagerlöf, and B. G. Svensson. 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. *Agriculture, Ecosystems & Environment* **77**:247-255.
- Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. *Oikos*:571-573.
- Tilman, D. 1999. Global environmental impacts of agricultural expansion: the need for sustainable and efficient practices. *Proceedings of the National Academy of Sciences* **96**:5995-6000.
- Tscharnkte, T., Y. Clough, T. C. Wanger, L. Jackson, I. Motzke, I. Perfecto, J. Vandermeer, and A. Whitbread. 2012. Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation* **151**:53-59.
- Tscharnkte, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecology Letters* **8**:857-874.
- Tuell, J. K., A. K. Fiedler, D. Landis, and R. Isaacs. 2014. Visitation by wild and managed bees (Hymenoptera: Apoidea) to eastern US native plants for use in conservation programs. *Environmental Entomology* **37**:707-718.
- Vaidya, C., K. Fisher, and J. Vandermeer. 2018. Colony development and reproductive success of bumblebees in an urban gradient. *Sustainability* **10**:1936.

- Walther-Hellwig, K., and R. Frankl. 2000. Foraging habitats and foraging distances of bumblebees, *Bombus* spp.(Hym., Apidae), in an agricultural landscape. *Journal of Applied Entomology* **124**:299-306.
- Watanabe, M. E. 1994. Pollination worries rise as honey bees decline. *Science* **265**:1170-1171.
- Westphal, C., I. Steffan-Dewenter, and T. Tscharntke. 2003. Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters* **6**:961-965.
- Westphal, C., I. Steffan-Dewenter, and T. Tscharntke. 2009. Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology* **46**:187-193.
- Westrich, P. 1996. Habitat requirements of central European bees and the problems of partial habitats. Pages 1-16 *in* Linnean Society Symposium Series. Academic Press Limited.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**:385-397.
- Wiens, J. A., and B. T. Milne. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecology* **3**:87-96.
- Williams, N. M., and C. Kremen. 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications* **17**:910-921.
- Williams, N. M., J. Regetz, and C. Kremen. 2012. Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. *Ecology* **93**:1049-1058.
- Winfree, R., R. Aguilar, D. P. Vázquez, G. LeBuhn, and M. A. Aizen. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* **90**:2068-2076.
- Winston, M. L., and L. H. Graf. 1982. Native Bee Pollinators of Berry Crops in the Fraser Valley of British Columbia. *Journal of the Entomological Society of British Columbia* **79**:14-20.
- Wolf, S., and R. F. A. Moritz. 2011. Foraging distance in *Bombus terrestris* L. (Hymenoptera: Apidae). *Apidologie* **39**:419-427.
- Xie, Z., J. Qiu, and X. Chen. 2013. Decline of nest site availability and nest density of underground bees along a distance gradient from human settlements. *Entomological Science* **16**:170-178.
- Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses. *Ecology* **89**:621-634.